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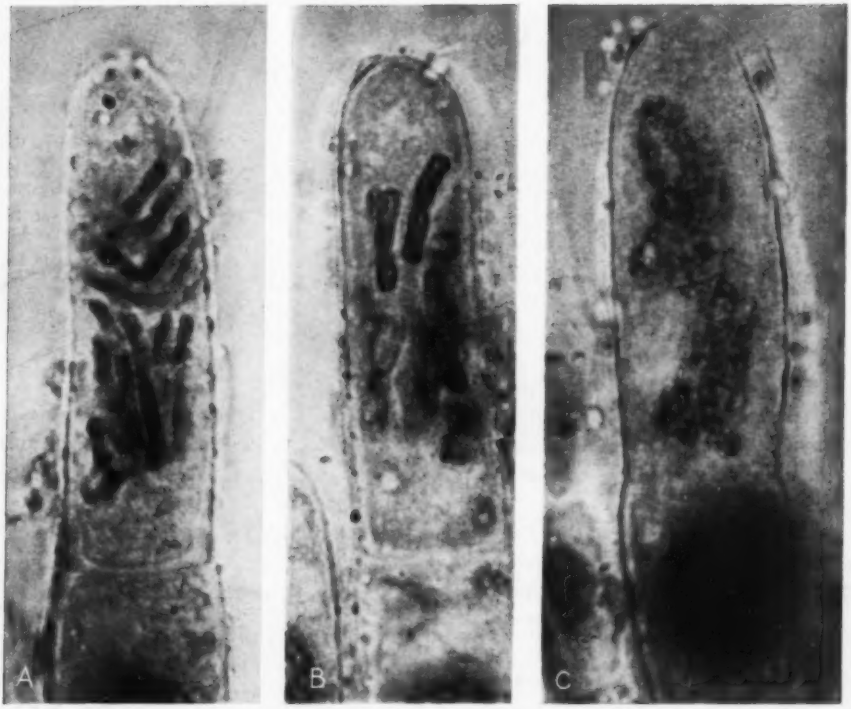

COLCHICINE-DOUBLED CHROMOSOMES
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A Revised Map of the X-Chromosome of Drosophila
Inheritance or Mosaic Resistance in Tobacco
More and Better(?) Human Race-Hybrids
Twins and Heredity vs Environment
"Bleeders" Without Hemophilia
Mongolian Yak-Cattle Hybrids
Dionnes Among the Goats
Hybrid Vigor in Hibiscus

VOLUME 29 JANUARY, 1938 NUMBER 1

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A COLCHICINE-INDUCED TETRAPLOID MARIGOLD

Frontispiece

Side and face views of two flower heads of the Gold Guinea marigold. The larger is from a tetraploid branch produced by treatment with colchicine. The smaller is from a normal untreated plant. Note the much increased size of the rays in the tetraploid plant. The distance between the arrows represents one inch.

THE CYTOLOGICAL AND GENETICAL SIGNIFICANCE OF COLCHICINE*

B. R. Nebel and M. L. Ruttle†

THE use of colchicine as an agent which might lead to induced polyploidy was mentioned to us by D. F. Jones at the A. A. A. S. meetings, at New Years, 1937. Preliminary experiments were started in April, after the then already fairly extensive literature on the use and action of the drug had been collected, part of which is cited here[1,3-7]. The Haskins Laboratory of Schenectady, N. Y., supported the work with a grant-in-aid.

Cytological Observations

Stamen hairs of *Tradescantia reflexa* Raf. were used to investigate the mechanism of chromosome doubling through colchicine.

Central parts of the buds of *T. reflexa* including the ovary and the attached filaments from which the pollen sacs had been removed were immersed in a culture solution in 5 cc shell vials. The culture solution contained the following constituents: cane sugar 1/34 M., KCl 1/100 M., $CaCl_2$ 1/1000 M., $MgCl_2$ 1/1000 M. To this colchicine was added in various concentrations. In concentrations of and above $10^{-4} \times 2$ molar‡ tetraploid nuclei are formed as shown in Figures 1 and 2. Colchicine specifically inhibits the formation of a spindle and thus blocks anaphase. All other phases of nuclear development continue. Due to the absence of a spindle the split metaphase half-chromosomes do not separate. The split chromosomes are held for a while in an atypical metaphase-like condition. (Figure 1*A*.) The chromosomes then commence to exhibit their chromonemata. (Figure 1*B*.) They become vesiculated. Adjacent chromosomes or chromosomal vesicles approach one another (Figure 1*C*) and a nucleus is thus reconstructed, the contours of which gradually become more spherical. (Figure 2.) Since each chromosome had divided before the nucleus was reconstructed, tetraploid nuclei are thus obtained. Higher degrees of polyploidy are obtained where entire plants are treated. Excised parts lack the vigor to show this.

Physiological Observations

Colchicine acts on every premetaphasic cell division present in stamen hairs kept in culture solution to which the drug has been added.

This means that wherever a cell was under the influence of the drug while in early, mid- or later prophase its nucleus becomes didiploid after metaphase. In this colchicine differs markedly from all other agents used to induce polyploidy.

A series of concentration experiments was carried out with stamen hair cells kept in culture solution for 14 hours. The following concentrations were observed: $10^{-4} \times 2, \times 4, \times 8$; $10^{-3} \times 8$; $10^{-2} \times 2, \times 4, \times 6, \times 8$, and 10^{-1} molar; no essential difference in effect was found within this extremely wide concentration range. Likewise cultures in colchicine $10^{-4} \times 2, \times 3, \times 4, \times 6, \times 8$ M. observed over 20 hours showed no essential difference.

It is thus suggested that colchicine, once a certain concentration is reached, destroys some link in the spindle-forming

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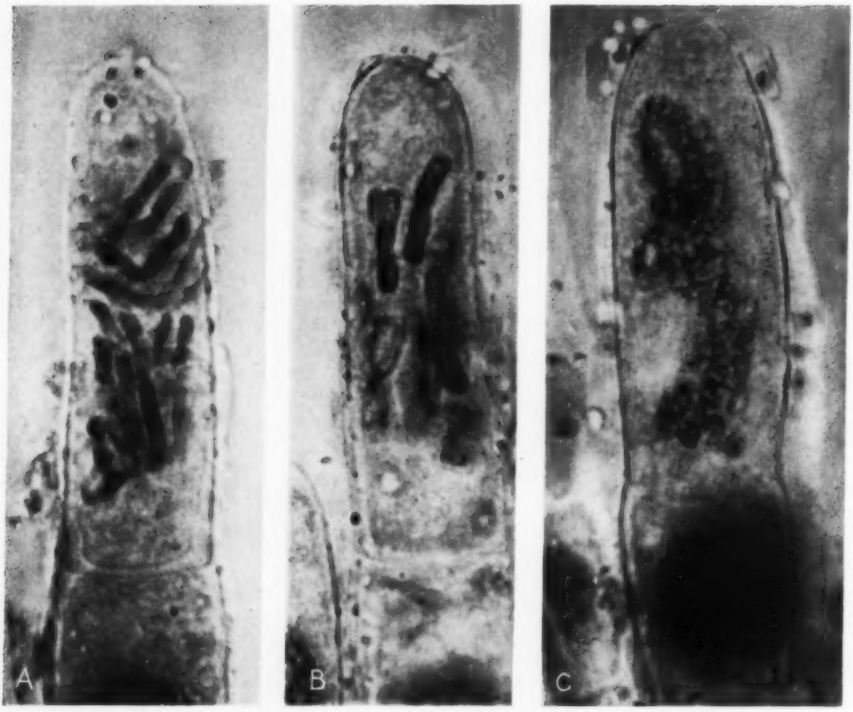
* The present summary is presented by invitation of the editor. Publication of the detailed data is planned elsewhere.

† Approved by the Director of the N. Y. State Agric. Experiment Station for publication as Journal Paper No. 242. Dec. 30, 1937.

‡ 10^{-4} m = 0.004% colchicine Mol. wt. = 399
10^{-3} m = 0.04 "
$10^{-3} \times 2$m = 0.08 " —, etc.



CHROMOSOME DOUBLING CAUSED BY INHIBITED SPINDLE FORMATION

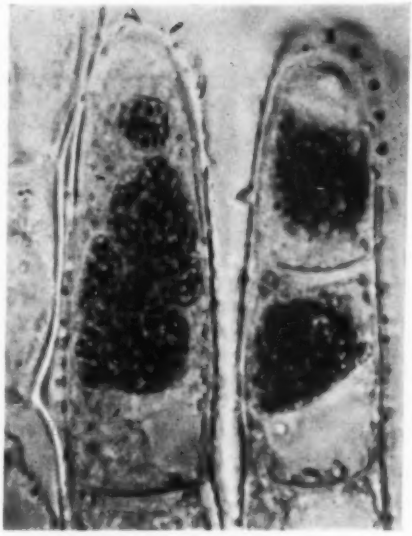
Figure 1

Stamen hair cells of *Tradescantia reflexa* under the action of colchicine. The drug inhibits the formation of a spindle. A didiploid nucleus is reconstructed inasmuch as the chromosomes multiply through splitting but the daughter chromosomes are not able to separate. *A*—Colchicine "metaphase" fixed in aceto-carmine. There are twelve "pairs" of chromosomes resembling 12 pairs of skis. The total chromosome number in the cell is thus raised from 12 to 24. *B*—The chromosomes are commencing to become "vesiculated," that is the chromonemata commence to show as they would normally at the end of anaphase. Note the complete absence of a spindle in *A* and *B*. *C*—The chromosomes have assumed the structure normally attained in a late telophase nucleus.

reaction. For Tradescantia stamen hairs in culture solution the lower limit of concentration resulting in the typical reaction lies just above 10^{-4} M. (0.004 per cent). It is remarkable that the addition of more drug does not cause other disturbances.

Cyclosis or streaming of protoplasm continues as in the control even when the concentrations of colchicine are far above that necessary to inhibit anaphase. For example streaming of protoplasm was observed to continue as in the control over a period of 21 hours in eight different concentrations of colchicine above 10^{-4} M. and up to 10^{-1} M. (4 per cent).

The effect of colchicine on nuclear divisions in stamen hair cells is not easily reversible. That is, the effect after 24 hours on anaphase is the same whether the stamen hairs are immersed in a cul-



NORMAL AND COLCHICINE INHIBITED DIVISIONS

Figure 2

On the right a normal division completed before the drug was applied; on the left a reconstructed didiploid nucleus. At the tip a "single pair of daughter chromosomes" forming a micronucleus.

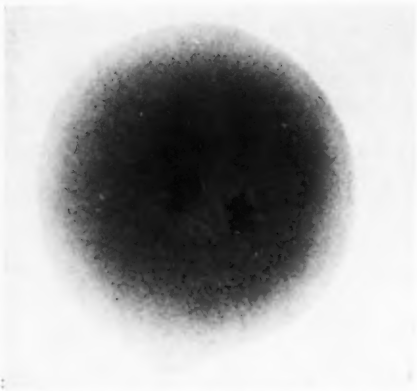
ture solution containing the drug for 1 hour, then transferred to a pure culture solution, or whether the stamen hairs remain in the drug-containing culture solution for 24 hours provided that effective concentrations of the drug were used. The following molar concentrations and time limits gave identical end results:

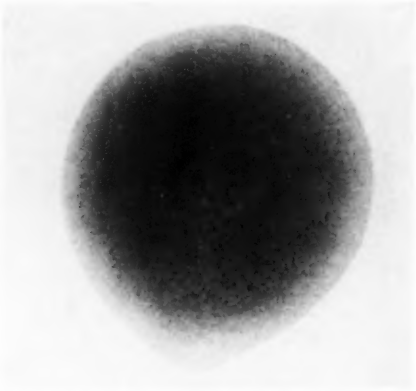
Colchicine	$10^{-4} \times 4$	1 hr.,	23 hrs.	pure solution
"	$10^{-4} \times 8$	"		"
"	$10^{-4} \times 4$	6 hrs.	18	"
"	$10^{-4} \times 8$	"		"
"	$10^{-3} \times 1$	"		"
"	$10^{-3} \times 2$	"		"
"	$10^{-3} \times 6$	"		"
"	$10^{-4} \times 8$	24 hrs.		–
"	$10^{-3} \times 1$	"		–
"	$10^{-3} \times 2$	"		–
"	$10^{-3} \times 6$	"		–

The stamen hair culture method may well be used to ascertain the effectiveness of a colchicine solution of unknown strength. The cells may be observed 90 minutes after immersion. Complete anaphase inhibition corresponds to concentrations of and above $10^{-4} \times 4$ M. Anaphase inhibition in about half the cells corresponds to $10^{-4} \times 3$ M. Slight inhibition after 90 minutes corresponds to $10^{-4} \times 2$ M. It is essential to use buds of the same age in corresponding counts. With three buds per vial significant counts of 200 or 300 cells can easily be made. We have used the first four cells from the apex of all living hairs for counting. In material killed with acetocarmine before counting the trained observer soon learns to distinguish between cells killed by the fixative and those fixed after death.

It is not to be expected that all higher plants and animals will be equally susceptible to colchicine. Studies carried out during June and July, 1937, in Woods Hole on the first division of the artificially inseminated eggs of *Arbacia punctulata* showed that the first cleavage division of this echinoderm is nearly ten times more sensitive to colchicine than *Tradescantia* stamen hairs. To observe the effect of the drug on *Arbacia*, colchicine was added to eggs in seawater cultures ten minutes after insemination. Concentration above $10^{-5} \times 2.8$ M. begin to prevent the first cleavage of the cytoplasm. Nuclear division is impaired above $10^{-5} \times 3.5$ M. With increasing concentration the following order of impairment occurs: cleavage fails, astral rays are gradually prevented from forming, the spindle is reduced in size and finally obliterated.

In *Arbacia* as in *Tradescantia* pseudodivision of the nucleus continues. Prolonged periods resembling metaphase alternate with periods in which the chromosomes become vesiculated forming abnormal resting nuclei. This is shown in Figure 3 taken from an egg fixed 135 minutes after fertilization and treated with $10^{-5} \times 5$ M. colchicine for 125 minutes. There is in this figure no cleavage. There have been several imperfect divisions of nuclear material, certain small groups of chromosomes have strayed from the main plate forming micro-nuclei, which in turn have gone through diminutive anaphases. Figure





COLCHICINE TREATMENT PREVENTS CLEAVAGE OF SEA URCHIN EGGS
Figure 3 **Figure 4**

Fertilized eggs of *Arbacia punctulata*. Colchicine $10^{-5} \times 5$ M. added 10 minutes after insemination. Mounts of whole eggs fixed after 135 minutes at 23° C. Note no indication of cleavage and absence of spindles and asters. Figure 3 shows irregular divisions of odd chromosome groups. In type the divisions correspond to the colchicine divisions of *Tradescantia* except that there is more scattering of chromosomes. With this concentration of colchicine diminutive anaphases may still occur. Figure 4 shows the same condition as Figure 3 except that the chromosomes have assumed interphasic structure. These colchicine interphases typically lack karyolymph and are for this reason difficult to see.

4 shows a sister cell of the one shown in Figure 3 exhibiting "poly-nucleate interphase."

Cytogenetic Observations

Seedlings in the early cotyledon stage or in the young seedling stage of the marigold varieties Gold Guinea, Dwarf, and Crown of Gold, of the tomato varieties John Baer, Oxheart and Rutgers Crop, of snapdragon, white clover, pinks, poppy, and petunia were treated by immersion of the shoots in .02 to .4 per cent aqueous solution of colchicine from one to 24 hours or by applying a thin film of 1 per cent colchicine in lanolin to the growing points. In the immersion method care was taken not to immerse the roots.

All treated seedlings except those immersed for a short period in the weaker solutions showed marked stunting and distinct thickening of the hypocotyl. Many treated seedlings failed to form shoots and died. If the injury was not too great the main shoot after some delay continued development or often a cluster of shoots formed above the cotyledons one or more of which eventually developed into main shoots. New leaves when formed were thickened, ridged, sometimes fasciated and often had irregularly chewed-appearing leaf margins. As the leaves developed, chlorophyll chimeras were frequent in certain genera. Later smooth normal-appearing leaves appeared and growth progressed as usual, or certain branches or even whole plants showed the characteristics of polyploidy typical of the species.

A cytological examination of the meristematic areas of seedlings fixed four hours after treatment in the cotyledon stage with a .2 per cent solution of colchicine for 3½ hours showed clumped metaphases but no cells with more than the normal chromosome number. Those fixed 40 hours after treatment showed irregularly shaped resting nuclei, giant cells with two or more nuclei, giant cells with one large nucleus having two or more nucleoli, numerous clumped metaphases, restitution metaphases, two metaphases side by side in one cell and cells

in metaphase containing the tetraploid or less often apparently the octoploid chromosome number. Some degeneration of chromosomes was evident in certain cells.

Marigold

The Frontispiece illustrates in the marigold var. Gold Guinea the difference between an induced tetraploid flower-bearing branch and a normal diploid branch. All parts of the didiploid branch are considerably enlarged, and the large rays are to be noted. This particular tetraploid branch was produced by treatment of the seedling in the four leaf stage for one hour in a .16 per cent solution of colchicine in the Tradescantia culture solution given on page 3. The roots were not immersed and are presumably diploid.

Of 18 marigolds of this variety treated in the four leaf stage with .02 to .16 per cent aqueous solution of colchicine for one to fourteen hours, seven plants showed evidence of tetraploidy in particular branches or in a large proportion of the plant. Cuttings from four of these plants have been made and the chromosome number in the root tips counted. In three the number approaches or equals the didiploid 48; in one plant one cutting had didiploid root tips and two had diploid root tips. It was thus established that colchicine may double the chromosome number in the plant to which it is applied (first generation) and this induced polyploid condition may be maintained through vegetative propagation.

Seed from individual flower-heads of three of the tetraploid and partly tetraploid plants have been planted. Chromosome counts from the root tips of these "second generation" colchicine seedlings show that the progeny (12 in number) from seed of two of the tetraploid plants are entirely tetraploid. Progeny from the third flower-head is composed of diploid and didiploid plants. This latter flower-head seems to have had an admixture of diploid and didiploid tissue. Chromosome counts from seedlings of untreated check plants showed the diploid number (24) in every case. These results show that seeds obtained from tetraploid flower-heads induced by colchicine may produce tetraploid plants.

Cytological evidence from micro- and macrosporogenesis and from pollen grain measurements corroborated the root tip findings. One of the treated plants, cuttings from which showed didiploid root tips, had mixed diploid and didiploid pollen grains in the same flower and diploid and didiploid tissue occurred in the ovary. Pollen grain measurements on this and other genera indicate that mixochimeras are relatively frequent.

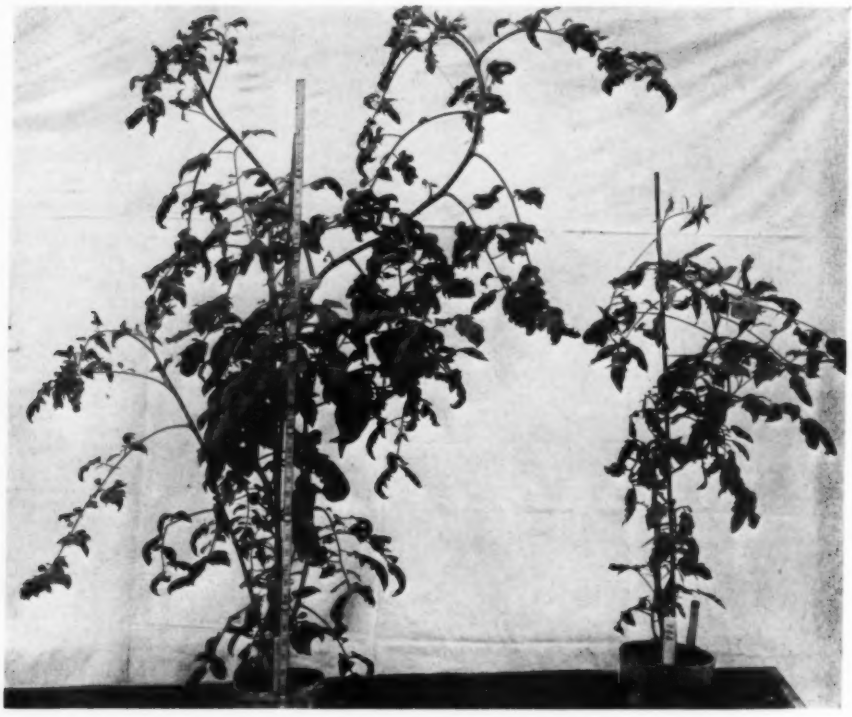
A large population of dwarf marigolds was also treated. These already have the tetraploid chromosome number and hence numerical octoploids should have been obtained. So far no octoploid seedlings have been selected although branches with thickened leaves and with flower heads having much enlarged involucres were frequent as were also chimeras in regard to flower color and shape.

Petunia

Seedlings of petunia in the rosette stage were painted with 1 per cent colchicine in lanolin. Certain of these treated plants produced shoots with tetraploid and higher chromosome numbers. Thus three plants have been examined having 14 chromosomes in the pollen grains as against 7 in the check. One branch of another plant has particularly small, much-thickened, rigid leaves and microspores with 18 to 29 chromosomes. Pollen from certain of the tetraploid branches was good, that from others poor. In all three tetraploid shoots studied there was, as evidenced from a measurement of the pollen grains, apparently some admixture of diploid tissue.

Snapdragon

An examination of snapdragon pollen from treated and untreated plants indicates the occurrence of tetraploidy as a result of treatment with colchicine. Giant pollen grains, from one plant tested, ger-



A STERILE TOMATO TETRAPLOID

Figure 5

Two tomato plants (var. Rutgers crop),—the larger is a tetraploid produced by applying a thin layer of 1 per cent colchicine in lanolin on the growing point of the young seedling, just as the cotyledons had well opened. The smaller plant is a normal diploid. The tetraploid is sterile and sets no fruit.

minated well. The germ tubes were very large as compared with the check.

Pinks

Fourteen Dianthus plants survived treatment in the early cotyledon stage with a .4 per cent solution of colchicine for 7 hours. Cuttings of three of these plants have been made; two plants of which have the tetraploid number (60) in the root tips of the cuttings and one has the normal diploid number (30).

Tomato

Tomatoes of three varieties were treated with colchicine in aqueous solution and with colchicine in lanolin (Figure 5.) From both types of treatment tetraploid plants were produced. The cells of root tips from cuttings of five of these plants have 48 chromosomes. Four of these five tetraploids have so far borne no fruit, a fifth has set fruit which may, however, have been on a diploid area. Chromosome counts from root tips of seedlings, the progeny of somewhat irregular treated plants, give so far only the diploid number (24).

Tradescantia reflexa

Cuttings of single clones were treated with .2 per cent colchicine for four hours.

Flower buds which developed one month later were examined. In untreated check cuttings the number of pairs of chromosomes at metaphase was uniformly 6. In most of the treated cuttings cells with 12 pairs of chromosomes occurred frequently at metaphase of the reduction divisions. Other cells of the same anthers had 6 pairs. Occasionally cells with 24 pairs of chromosomes were found. The chromosome count in one pollen grain was thirty chromosomes.

Conclusions

Colchicine inhibits spindle formation. In dividing cells of animals and higher plants, cells with the doubled chromosome number are thus formed. As growth progresses in plants, didiploid and mixochimeric shoots are formed. Tetraploids have been obtained by this means in many genera of herbaceous plants. Various genera do not show the effect of polyploidy equally well.

To induce chromosomal changes in somatic tissues of cultivated plants as obtained with colchicine may be called plant breeding with non-Mendelian methods. It must be emphasized that this method of genetical approach will require more care on the part of the practical breeder and more expense than the Mendelian method if it is to lead to permanent progress on a broad front.

It has been stated that the higher degrees of polyploidy may in certain species of cultivated plants not lead to forms of greater economic value. This question can not be answered before polyploid populations have been observed which are in size comparable to the now existing diploid populations of the species under discussion.

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◆

THE FECUNDITY OF HEREDITARY DEFECTIVES

TWO German surgeons concerned with enforcing the sterilization law in Berlin have taken advantage of their opportunities to make an important contribution to the study of fecundity.

Several studies have been published previously, of the spermatozoa of normal men. This book* offers a study of the spermatozoa of men who had been diagnosed as hereditarily defective. At the time of the operation, the upper part of the vas deferens was washed out, and the sperm thus obtained were studied in great detail, 20 different types of abnormality being distinguished.

In their control studied, the normal man is found to produce 19% of morphologically defective sperm. By

*Stiasny, H., and K. D. J. Generales, Jr. Erbkrankheit und Fertilitaet. Pp. 175 with 60 illus., many in colors. Price, bound, RM 29. Ferdinand Enke Verlag, Stuttgart, 1937.

contrast, the chronic alcoholic patient produces 75% of defective sperm.

Previously it has been assumed that as much as 25% or 30% of abnormal sperm were a good evidence of lowered fertility if not of sterility. But the fertility of these chronic alcoholics was not diminished, the authors claim.

In cases of inherited mental defect, 62% of abnormal sperm were produced, accompanied by low fecundity, — as is the case generally with the mentally defective male. On the other hand, in hereditary deafness 62%, and in hereditary blindness 75%, of defective sperm appeared.

It is easy to find a theoretical reason for the production of a high proportion of defective sperm in the chronic alcoholic, or in the mentally defective with his far-reaching constitutional deficiencies. It is not so easy to understand why congenital deafness or blindness should be associated with equal or greater production of defective spermatozoa. The authors ascribe the result to the inactive sex life of the patients, which in turn results from the inherited handicap; but this seems to be wholly speculative.

Epilepsy and Schizophrenia, both supposed to be constitutional in origin, show less abnormality of spermatozoa (58% and 54% respectively) than blindness and deafness.

The study is apparently based on 126 men sterilized under the German law,— a small number for statistical purposes. It is greatly to be desired that the authors' work be repeated on a much larger scale. If their conclusions are confirmed, it will necessitate some changes in present ideas concerning reproduction.

The point I have mentioned is only one of many described in this book, which gives a review of sterilization, and of the anatomy and physiology of the male reproductive tract. It is of first-rate importance in the study of the biological basis of eugenics.

PAUL POPENOE

Institute of Family Relations, Los Angeles, California

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Lethal Genes in Poultry

TO THE EDITOR:

IN a publication on "lethal characters" by O. N. Eaton in a recent issue of the JOURNAL various statements occur which may be misunderstood on account of brevity of presentation or which are erroneous. In view of the widespread use which is made of such review articles, the following comments are made with reference to the section dealing with "Poultry."

There is no proof that "chondrodystrophy" is a "recessive involving three pairs of factors"; in fact, there is no critical proof that the condition is inherited. Chondrodystrophy has nothing whatever in common with "foetal malpositions", and it is difficult to see why they should be mentioned in this connection. The "Creeper" mutation is dominant with *recessive* lethal effect. "Dwarf" is a recessive, as stated, hence all dwarfs are homozygous. The writer knows of no proof for the statement that the abnormalities of various types, referred to as "embryonic lethals", are "due to breeding" or that they are inherited. There is evidence suggesting that the majority of these abnormalities is not hereditary. "Flightless" is dominant not recessive; it may have a partial recessive lethal effect (cf. reference to Creeper above). There is evidence that "malposition of embryos" is not a lethal factor. The lethal reported by Dunn in White Wyandottes is not identical with the gene for recessive white; it appears to be closely linked to it. Hence, it is not justified to say that "homozygous whites die". The Cornish lethal, referred to as "short legs", is due to a single recessive factor; it is entirely independent of the Creeper mutation, not "perhaps associated" with it.

The other sections of Eaton's paper have not been checked by the writer.

WALTER LANDAUER

Storrs, Conn.

One error cited is due to a misprint; which the editor regrets: "Embryonic Lethals" were cited as due to *inbreeding*, — not to *breeding*, the implication being that recessive factors are involved.—ED.

A REVISED MAP OF THE SALIVARY GLAND X-CHROMOSOME

of *Drosophila Melanogaster*

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THE present revision of the map of the salivary X-chromosome shows the additional detail that has been made out since the earlier maps were published by Painter[5] and by Bridges.[1] Many new lines, mostly faint, have been observed, and many of those previously mapped have been resolved into doublets. The characteristics and relative intensities of most lines are represented better. A great convenience is the numbering of all mapped lines, even the faintest, a feature which allows concise reference without ambiguity or lengthy description. The map of 1935 will continue to serve as a guide map, since the major features and coordinate system of divisions and subdivisions stand. But it had still been found necessary, in analyzing each specific aberration, to supplement the published map by special study of the normal banding of the region involved. The present map meets this difficulty adequately, but will ultimately need further revision in certain difficult regions, notably the inert region, and will need supplementing by a table or map showing the proportionate distances of the entirely lax chromosome.

Method of Revision

While the former maps were based on temporary aceto-carmine preparations, the material used in the revision has been exclusively permanents. A method of making permanents of high quality (DIS-6) has permitted the accumulation of large numbers of slides which could be compared at leisure and from which the best were selected for intensive study. These slides are being kept for rechecking of detail whenever a question may arise. The higher refractive index of the euparal mounting medium, as compared with the acetic-acid and water mounting of temporaries, results in superior transparency and definition.

The preparations were from larvae raised to maximum size through supplying extra yeast to limited numbers of larvae per culture at low temperature (17°-19°). Since the number of cells in each larval tissue is established very early and subsequent growth is mainly by increase in size of cells, the largest larvae yield the largest chromosomes. The selected larvae were prechilled and then chilled Ringer's and aceto-carmine were used for dissection and fixation. The chilling seems to give sharper firmer outlines and the heavy bands as close doublets instead of inflated capsules, possibly through a slower fixation which allows the escape of more fluid from within the chromosomes and bands.

Fixation for twenty minutes to one hour preceded smearing on albuminized slides. Dehydration was by vapor from 95% alcohol, and mounting was in euparal directly from the 95% alcohol bath in which the covers were wedged off.

On selected slides especially favorable in fixation, staining, and large size of chromosomes, search was made for *X*-chromosomes where large sections were free from kinks and were uniformly stretched to the greatest extent compatible with retention of normal structure. From six or more of the best of

such registered chromosomes, camera lucida drawings at 5,000 diameters were made for each of the twenty divisions. A generalized map was then made by comparison of these drawings and rechecking disagreements in number or character of bands. For the dimensions of the generalized map, arithmetical averages were made of the distances between the main bands, including all those demarking each section and subsection. Similarly, the chromosomal diameter at each of the 120 subdivision points was found by averages from these same drawings. The characteristics and intensities of each band and line were then drawn in from comparison of the different drawings of each region. Disagreements between the former maps and the new were rechecked.

The previous limits for the divisions and subdivisions were found satisfactory in all except a few cases. Such slightly changed demarkation points are indicated on the new map by dash instead of solid lines. The demarkation point is put in all cases just to the left of a conspicuous or well-defined band.

Characteristics of the New Map

The new map shows 1,024 numbered lines, as compared with 725 on the 1935 map. The length of the new map is 414 microns as compared with 220 microns for the old. This difference in length is partly due to choice of larger chromosomes and partly to greater and more uniform stretch. In using the map it should not be forgotten that smaller chromosomes and less stretch will fail to show all the faint bands and that many doublets will appear single.

Certain regions of the chromosome are especially hard to analyze. Of these the most difficult is the basal region (division 20) or chromocentric portion, probably corresponding to the heterochromatic or inert region of the prophase and metaphase *X*. The banding is much more diffuse and irregular here than at any other region, with the chromosome tending to show separate strands instead of a smooth bundle. The chromomeric granules are loosely separated with ragged outline and clotted appearance. It is not felt that this region is satisfactorily worked out, although the revision agrees substantially with the analysis by Prokofyeva-Belgovskaya.

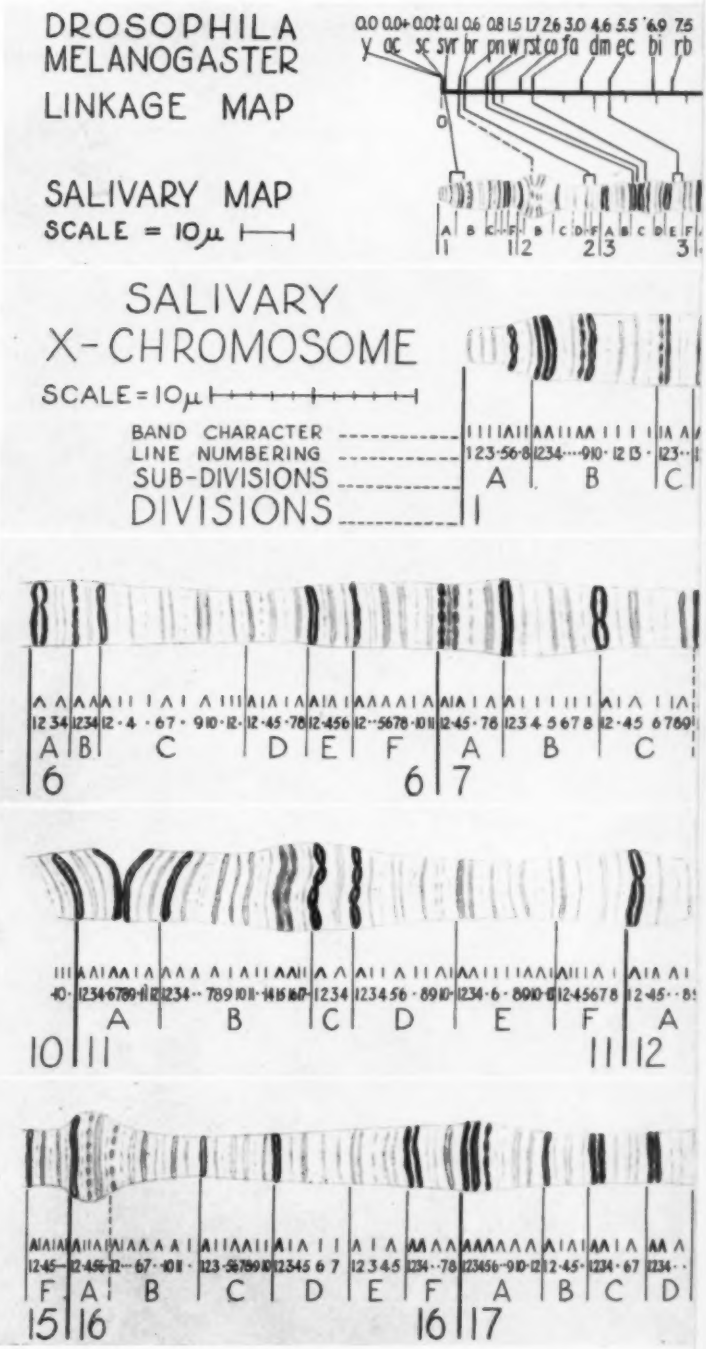
The huge bag-like nucleolus seems most often to be dependent from, or intercalated in, the chromocentric region at 20B-C. Secondary bodies of nucleolus-like type may be seen not infrequently as rounded exudates from the partly broken-open offset at *19E* or the weak point in *11A*.

The second most difficult region is in *12D-E*, where the banding is usually complexly distorted and diagonally intersynapsed. It seems probable that this region involves a reversed repeat. Nearly as difficult of analysis is *11A*, also probably a reversed repeat centering on heavy paired doublets which form a very weak place in the chromosome, often breaking entirely across. Two other reversed repeats, with confused clumping due to synapsis of homologous bands along the chromosome, are in *2B* and *3C*. The *2B* region is further modified by the "puff" or inflated bulbous region. The *3C* region has great significance as the seat of white and other important loci and also of unusually high crossing-over. A very faint band drawn between the two inner bands must be regarded as doubtful (although in two cases of extreme stretch it might be interpreted as present as a doublet).

Other places having the appearance of reversed repeats are in *8B* and *9A*, though the four bands of *9A* rarely, if ever, show the confused synapsis common in *2B*, *3C*, *11A* and *12E*. No critical study has been made as yet of these and some other regions suspected of being repeats.

The Physical Structure of the Chromosome

The subdivision of many bands into segments or dots and the longitudinal alignment of these dots through series



Supplement to *Journal of Heredity*, Vol. 29, No. 1, January, 1938. (To foll
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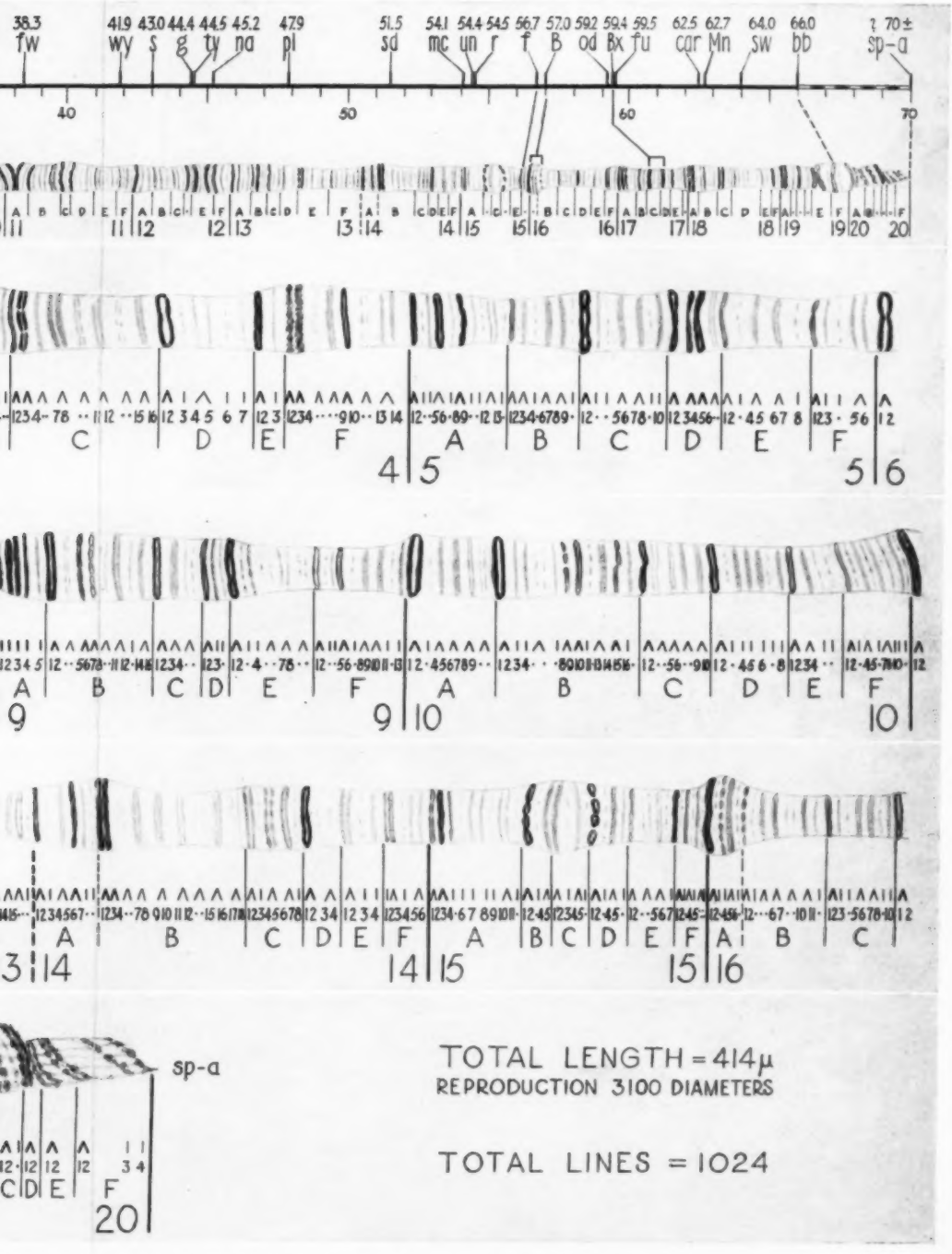
REFERENCE MAP OF THE SALIVARY GL



IVARY GLAND X-CHROMOSOME OF *DROSOPHILA MELANOGASTER.*

Figure 6

of adjacent bands have been interpreted as evidence of compound structure of the salivary chromosomes. The salivary chromosome is thus essentially a bundle of parallel chromonemal threads, similar to that of ordinary chromosomes except that the number of strands is supposedly higher and the spiral coiling has practically vanished. The lower limit of the number of individual strands present would be the visual number of dots in the finest-grained bands, probably eight per homolog, though the largest cells suggest sixteen. The upper limit is far more problematical, since a visual separation of individual strands does not occur at all in some bands and extends variously to two, three or four stages in the coarsely segmented dashed and dotted lines. Furthermore, in the salivary chromosomes the chromonemata may grow to far greater size without becoming unstable and dividing. Also the large size of the chromosome may be partly due to relatively great amounts of fluid between the chromonemata. Hence, the upper limit for true chromosomal strands may be only a stage or two above the greatest visual subdivision.

Not more than about a tenth of the length of the lax salivary chromosome could be readily accounted for by simple uncoiling of metaphase chromonemata. Considerations of growth by surface accretion and reproduction by simple splitting incline to fiber-like crystals as models of gene structure. On this view the remaining increase in length would not be through lengthening of gene material but could be by indefinite extension of relatively unorganized intergenic connective substance.

Observation of stretched salivary chromosomes shows, in comparison to lax chromosomes, that most of the elastic yielding comes in the unstained material between bands. The bands move further apart and may separate into component lines but do not lose their characteristic narrowness. The regions of lightest bands generally stretch most and become slimmest, while the dark-banded regions of the chromosomes are relatively inelastic and retain their large diameters better. Thus both stainability and high physical strength characterize the nucleic-acid bands, while the regions low in nucleic-acid stretch like rubber.

Correspondence Points Between the Linkage and Salivary Maps

For comparison of the linkage and chromosome maps the upper line of the figure gives the latest revision (August 1937) of the X-chromosome linkage map, as sent to *Tabulae Biologicae* for publication. The lower line gives the present salivary revision at one-third the linear magnification of the detailed map below. The correspondence connections drawn as solid lines are from Painter[5] and especially Mackenson[4] in the cases of the *y-sc, pn, w-fa, ec, v, f* and *Bx* regions. The localization of cut is from Hoover[3] and Bar from Bridges.[2] The regional localization of miniature is from unpublished studies by Demerec on deficiency 259-4, which includes miniature but not dusky. Slizinski has contributed unpublished salivary localizations of four lethal deficiencies (304-69 in *4C;* 291-3 in *5D;* 291-69 in *7E* and 291-7 in *8B*) but does not regard the genetic localizations as adequately studied. Schultz had found (unpublished) that the locus of broad is probably in the bulb and that bobbed is at *19F,* though Prokofyeva's (1937) location for *bb* is at *20C or 20D.*

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A HEREDITARY CASE OF A PECULIAR HEMORRHAGIC DIATHESIS

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IN addition to the clinically and genetically clearly defined hemophilia, the clinically thoroughly worked out Werlhoff's disease, and a whole series of purpura, we meet with cases of hemorrhagic diatheses which are difficult or sometimes impossible to fit under the heading of one or another of the existing classifications.

Within recent years several such cases have been published, being described in the literature under the various names of thrombasthenia, thrombopathia, purpura and pseudohemophilia, being classified by a number of hematologists as belonging to the general group of thrombopathia.

Common features of all these cases are the tendency to easy bleeding, lengthened bleeding time in the presence of a practically normal number of thrombocytes, normal coagulation time, and so on. However, together with these general characteristics there are marked differences in the number of thrombocytes, character of clot retraction and force and localization of bleeding. Notwithstanding the fact that in every case the same autosomal type of inheritance is observed, it may be suggested that these cases are genotypically dissimilar, since there is a much greater resemblance in cases within a family than in cases from different families. The latter, however, is not absolute. In the majority of cases intra-familial similarity of the location of the lesion is absent (Glanzmann, Willebrand and Jürgens, Giffin, Minot, Rothman and Nixon, Rosling, Farber, Levit and Malkova), while in other cases it is observed (Curshman, Minot, Little and Ayres).

The familial case of hemorrhagic diathesis observed by us and presented below, was followed through four generations; (Fig. 7). It may be regarded as belonging to the second group of cases, having identical localization in the various members of the family.

1. *A.*, 23 yrs. (III, 18), entered the Central Institute of Hematology and Blood Transfusion for relief from attacks of hemorrhage from the throat occurring every year or half-year, preeminently during hot weather following overexertion, much talking or even without apparent cause. The blood is liquid, bright-red, sometimes with, sometimes without clots and is lost to the amount of one or two glassfuls, spouting out, in the patient's words, "like a fountain."

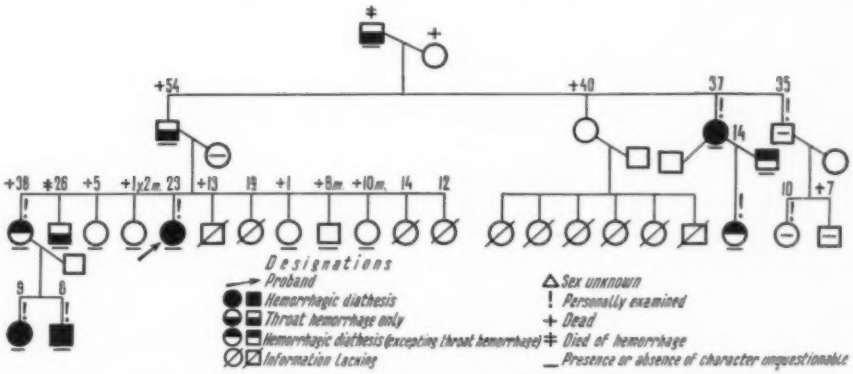
The patient's anamnesis indicates bleeding of the gums and occurrence of black-and-blue spots on the body since childhood; menstrual flow copious.

Throat hemorrhages began at 18 years of age. Blood—analysis: Hb.—63%, Er.—4,300,000, L.—8,200. Bleeding time 8 minutes. Thrombocytes—96,200. Moderate hypochromia.

2. *S.*, brother of the proband, (III, 15). Died at the age of 26, according to the family's statements, at the Sklifassovski Emergency Hospital (Moscow) following a throat hemorrhage.

3. *P.*, sister of the proband, (III, 13). From childhood affected with bleeding of the gums and black-and-blue spots on the body. No acute attacks of bleeding or throat hemorrhage noted. Blood analysis: Hb.—61%, Er.—4,880,000, thrombocytes—117,000. Bleeding and coagulation time—normal.

4. *V.*, 9 yrs. old, (IV, 7), niece of the proband. Affected with bleeding of the gums, black-and-blue spots on the body and throat hemorrhages since early childhood. Blood analysis: Hb.—62%, Er.—4,380,000, thrombocytes—135,000. Bleeding and coagulation time—normal.



FOUR GENERATIONS OF A TENDENCY TOWARD HEMORRHOGES

Figure 7

The occurrence of hemorrhages under the skin of the throat and elsewhere in members of this family shows direct transmission through either sex.

5. *S.*, 8 years old, (IV, 8), nephew, the proband. Symptoms like those of his sister, only more marked and more frequent. Blood analysis: Hb.—57%, Er.—4,610,000, thrombocytes—161,000. Bleeding and coagulation time—normal.

6. *P.*, (II, 8), father of the proband. Suffered in youth from frequent throat hemorrhages and occasional nose bleeds. At age of 54 died of pneumonia.

7. *P.*, (I, 1), grandfather of the proband. According to relatives, died of throat hemorrhage.

8. *S.*, (II, 4), proband's aunt on the father's side. From childhood notes bleeding of the gums when brushing teeth. Spontaneous purpura. Following extraction of a tooth, bleeding continued for a month. At age of 25 had gastro-intestinal hemorrhages daily for a month. At age of 37, intestinal hemorrhages again occurred, repeating 4 or 5 times a day, with throat hemorrhages once a day, for a period of one month. Since then the hemorrhages occur nearly every year, not infrequently causing the patient to lose consciousness. Blood analysis made during period of illness: Hb.—45%, Er.—2,500,000, L.—4,000, thrombocytes — 100,000. Coagulation time—25 seconds (Fonio method), Retraction—0,9 (S. G. Levit's method). Bleeding time—5 minutes. Analysis of gastric juice—free HCI absent, total acidity—20. Otherwise normal.

9. *L.*, (III, 11), daughter of patient II, 4. Black-and-blue spots on the body first appeared at age of 14. Gums bleed. Bleeding time 6 minutes. Hb.—86%, Er.—3,000,000, thrombocytes—120,000.

Six of the above described individuals were examined in the Institute for gastric or duodenal ulcers. All findings were negative.

The proband's uncle (II, 7) and his family, likewise all deceased brothers and sisters of the proband exhibited no signs of diathesis. Regarding the other brothers and sisters (III, 20, 24, 25), the proband's aunt (II, 1) and the latter's family, we were unable to secure the necessary data.

Turning to an analysis of the given case, it would seem that we have to do here with a very peculiar form of hereditary diathesis. Its peculiarity lies in the localization of the lesion—throat hemorrhage being the chief clinical symptom, manifesting itself in this case in the same way in nearly all affected members of the family during several generations.

It might be supposed that we have here a special form of Werlhoff's disease characterized by the occurrence of throat hemorrhages (which although rare, have nevertheless been described). That this cannot be the case here is proved by the absence of Thrombopenia, so characteristic of Werlhoff's disease, and by the occurrence of individuals affected with throat hemorrhages but not with purpura or bleeding of the gums. It should be remarked however that all the patients except II, 4 were examined

during periods of remission, when even in patients suffering from Werlhoff's disease the number of thrombocytes often becomes normal.

Both sexes are affected alike. The disease manifests itself at various ages.

If we assume that the disease is caused by one conditionally dominant gene (the term conditionally dominant is used to designate those genes whose phenotypical make-up in the homozygote is not known—Levit), then, at least in case of complete manifestation, half the children from marriages where one partner is affected should likewise be affected. In our case, the proportion of affected individuals (6) persons) to healthy ones (7 persons) is 1:1 (although it must be noted that 5 of the 7 healthy individuals died in early childhood, when the disease might not yet have had time to appear.* This ratio indicates that we have here a monohybrid conditionally dominant disease.

As regards the simultaneous presence of both throat hemorrhages and other manifestations of hemorrhagic diathesis in one and the same individuals, chance coincidence may be the explanation. This seems very probable in view of the frequency of cases of slight bleeding among the population. According to Levit and Malkova, doubtful and very light forms of bleeding are met with in 33.1% of the male and 42.1% of the female population. In this event, patient III, 25 may be regarded as a latent carrier of the gene under consideration.

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German Marriage Loan Fund

More than 636,000 young German couples have availed themselves of their government's Marriage Loan offer, with the marriage rate itself having increased from 510,000 in 1932 to 740,000 in 1934. Since enactment of the new law (1933), abortions have decreased 40 to 60%.

Among these 636,000 borrowers, 220,800 children have been recorded, each of whom entitles the parent to cancellation of one-quarter of their loan. Loans amount to $200-480; and the birth of four children in a family therefore effects a gift from the government in this amount.—*Amer. Eugenic Soc.*

*Four others are not included in the calculations since no information as to their health is available.

DIONNES OF THE GOAT WORLD

THIRD QUINTS

Figure 8

These five healthy kids are this billy's third venture in quintuplet paternity, according to his owner Miss Lucy Pinder of Pasadena, California.

CAPRINE vital statistics are less adequate even than those of man, so that few data are available regarding the frequency of multiple births among goats. The birth of quintuplets, all of which survive, is admitted to be extremely rare, and deserving of record. This five-times-blessed event has occurred twice in recent months, and in both instances under conditions which suggest a genetic tendency toward multiplet production.

The first set of quintuplets occurred in a flock of goats owned by Lucy Pinder, of Pasadena, California. The case is even more remarkable in that this is the

FIVE AMERO-NUBIANS
Figure 9

Not content with three sets of triplets in earlier years, Mr. Patt's doe bore quints in March, 1937. The Nubian sire was from a notably fecund strain.

third litter of goat quintuplets credited to the father, whose supercilious expression, as recorded in Figure 8, thus has ample justification. His achievement puts one in mind of the current fable concerning Papa Dionne and the loving cup presented by a group of admiring fathers. The great man is said to have eyed it speculatively, and to have asked: "Is it mine, or do I have to win it three years in a row?"

The second instance of quintuplets in goats was brought to light by a note questioning the actuality of Peter Poth's alleged sextuplets in cattle in *Time* magazine. Mr. Roscoe F. Patt of Reading, Pennsylvania, gave the following account of another instance of outstanding fecundity in milking goats:

November 1, 1937

Replying to your letter of the 26th of October regarding goat multiplets, I will try to give you some of the pertinent background which bears on last spring's birth rate in my son's herd.

Birth weights of Goat Kids—Herd of Wm. N. Patt, 2nd, West Leesport, Pennsylvania, March, 1937. Sire purebred Anglo Nubian buck (Prophetically named Abou ben Adam).

Dam No. 1	Dam No. 2	Dam No. 3	Dam No. 4
Common American doe previous record 3 sets triplets	½ grade Nubian previous record 1 set twins	grade Nubian previous record 1 set twins	⅞ grade Nubian 1st kindling
Buck 3 lbs. 6 oz.	Doe 5 lbs.	Doe 6 lbs. 14 oz.	Doe 9 lbs.
" 3 lbs.	" 5 lbs.		
" 2 lbs. 8 oz.	" 4 lbs.	" 7 lbs. 2 oz.	
" 2 lbs. 8 oz.			
Doe 2 lbs. 2 oz.	Tot. 14 lbs.	Tot. 14 lbs.	
Tot. 13 lbs. 8 oz.			

The remainder of the herd freshened some weeks later and were not recorded. About equally divided between single kids and twins of normal size, bucks predominating.

First we moved in October [1936] to a farm badly run down and very poor for real farming but containing some 50 acres of goat paradise. The herd was in good condition but had been closely confined and the new quarters and over abundance of pasture with the opportunity for exercise all coming at the height of the natural breeding season made them somewhat unmanageable when the does came in season. The herd sire, a young powerful purebred Nubian, broke loose several times and the does were bred earlier in the season than we had planned, (winter and early spring kids are a burden to raise). I believe there is some basis of fact in the practice among sheepmen of suddenly increasing the quality and quantity of feed given breeding ewes, just before they are due in season, to increase fecundity. The interval between heats in the does is 21 days and the does bred at the second or third heats, after moving to the farm, returned to the natural number of one or two kids. These were served by buck after the cream of the new pasture had been eaten and winter had made it more difficult to get. The multiplets were produced by matings made after some two weeks of abundant feed. The boy's records may be somewhat sketchy but I was interested enough to insist on recording the weights of the kids in the case of the multiple births. I will enclose a table of data from his records.

The doe producing the quints clearly carries an inherited ability to produce multiplets. She is one of triplets from a mother by son breeding and in her four times bred has produced three sets of triplets and one of quintuplets. She was purchased very young and bottle raised and was made quite a pet. As a result she is very pugnacious with her herd mates and shows a devilish ingenuity at getting to the buck when she is in season. For this reason she is invariably bred to kindle in cold weather and has been in one fight which caused her to kid prematurely. Her kids have been perfectly normal but some of her earlier ones did not live to maturity. She obligingly dropped the quints on a Saturday afternoon with the whole family ready to assist. Undoubtedly some of the five could not have survived unassisted. Competition almost eliminated the smallest even so. She is not an extra good milker, is somewhat undersized and possibly would have gone to the butcher if her multiplets had not kept us curious as to what she would produce each year. The one daughter we know about had not produced extra numbers of kids. Her quality is such that for milking stock it would be a waste to save one of her buck kids for breeding. As a matter of curiosity I would like to know whether the multiple producing factor is a simple inheritance and whether it could be a sex linked inheritance possible to perpetuate only through her male offspring, or as is possible she is just a freak with some abnormal internal arrangement of her reproductive equipment. The enclosed snapshot was taken when the kids were several weeks old by the county extension agent. The discrepancy in size was rapidly narrowed as soon as the kids began to take on any quantity of feed.

It is my opinion from somewhat incomplete data that multiplets tend to be a few days premature and that single kids are apt to be a bit too large and give some trouble at birth. I have assumed that simple solid geometry is the answer to this.

I hope this gives you the information you wish and not too much irrelevant material. I have been unable to get the print taken at two days of age by the photographer of the local *Reading Eagle*. This shows the new born quints with the drooping "hound" ears of their Nubian sire. In the later print you will notice they have stiffened into over-sized prick ears more like their dam. The Nubian-common cross usually shows much more of the Nubian breed character particularly the large hound ears and Roman nosed profile. The quints as far as appearance goes are all common goat.

Very truly yours,
ROSCOE F. PATT.
Reading, Pa.

The genetic factors underlying a tendency to multiple births in mammals are not clearly understood. Breed, and racial differences in twinning frequency are recognized in livestock and in the human race. Thus dairy cattle have been shown to produce twins at a significantly higher rate than the beef breeds (*Jol. Dairy Sci.* 3:260-290, 1928). Strains of cattle have been recorded in which an unusually high percentage of twins births occurred, suggesting a rather simple mendelian inheritance. (*Jol. Hered.* 16:273-279, 1925).

A paternal influence on the occurrence of multiple births is a subject that has received some scientific attention and some evidence has been adduced of an inheritance of the twinning tendency in the male line. (*Journal of Heredity* 28: 322-323. 1933). Should there prove to be a "quintuplet gene" in goats, the sons of this thrice-blessed billy may revolutionize the goat industry.

One of the most ambitious attempts to breed a twin-bearing strain of livestock was that carried on for many years by Dr. Alexander Graham Bell. Here persistent selection of multi-nippled twin-

bearing ewes, and of rams of twin-bearing ewes, was not effective in evolving a twin-bearing strain. Castle, who analyzed Bell's records (*Journal of Heredity* 15:75-85, 1924) discussed the experiment at length, and concluded that selection had not increased the percentage of multiple births, the major factor probably being "the state of nutrition of the mother, which is affected (a) by her age; (b) by the season of breeding, which in turn probably acts through (c) the food supply. . . . It is probable that the only factors concerned in twinning in sheep are those which affect the general vigor of the mother, causing multiple rather than single ovulations." The same reasoning would seem to account for the unusual fecundity of the Patt goats, where entrance into a "goat paradise" just at breeding time was immediately reflected in a concerted movement to people the earth with bigger and better goats.—R. C.

Mr. Patt comments as follows on the proof of the above article:

I do question your conclusions as to the cause of the multiplets being entirely environmental. It is true that, genetically, milk breeds of goats are twin bearing. A doe normally bearing twins might occasionally bear triplets under exceptionally favorable conditions and I suppose the quints from a triplet bearing doe can be so explained but a doe repeatedly bearing more than the usual two particularly as she is one of triplets and the result of dam to son inbreeding, must be genetically different from the normal. The dam and the quintuplet doe are now bred to kindle this spring and we are very interested in the outcome. If there are more than the usual two I would like to continue the breeding experiment by using one of the multiplet bucks. I have a suspicion that this trait is transmitted from granddam to granddaughter through the male, as is the case to a large extent with high milk production, egg yield, etc., which in the last analysis are the result of abnormal development of the reproductive organs.

These quintuplets are a freak and cause interest because of the Dionne five, making any quintuplets news. I believe there is an authenticated case of a doe producing eleven kids within twelve months, that is, a set of five and one of six. I can locate it in one of the Dairy Goat Journals if you wish or perhaps you could be flooded with instances of extra large litters if you communicated with the registry associations.

In view of the failure of Dr. Bell's experiment, the editor must be pardoned for discounting heredity as a major cause of the hyper-fecundity of Mr. Patt's goats. He will be delighted to admit his error if quintuplets become the rule rather than the exception in this herd. Very possibly the close inbreeding has fixed a genetic tendency toward the production of litters rather than twins or triplets. We shall await with interest reports on later generations.—R. C.

Psychopathic Breakdowns

THE author of this short monograph* believes that it is justified to establish anxiety psychosis as a separate psychopathic entity. There is no doubt that the symptomatology of the cases which are reviewed suggests great similarity, and also that these cases differ from manic-depressive or other well known psychoses. Final judgment in this respect must be left to psychiatrists. Evidence is presented for the hereditary nature of this condition, though the mode of inheritance cannot be established at present. In addition, a review is given of depressive conditions brought on by sexual involution. These are not uncommon in women, beginning at or shortly after the onset of the menopause, but it is not certain whether or not corresponding psychoses occur in men.

WALTER LANDAUER.

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*LEONHARD, K. *Involutive und idiopathische Angstdepression in Klinik und Erblichkeit* (Clinical and genetic observations on involutionary and idiopathic anxiety depressions). Publishers: Georg Thieme, Leipzig, 1937. 116 pp. Price: 7 marks, less 25%.

TWIN LIGHT ON NATURE VERSUS NURTURE

A Review of *Twins*

SIR JAMES JEANS, in one of his writings, remarks that it is frequently easier to get some sort of an answer from nature to a nonsensical question than it is to frame a sensible question to begin with. The authors of this book* are to be commended for propounding a question in a sensible form. They seek, through a study of twins, to determine how much of the variation in certain traits is due to differences in the genetic compositions of the individuals, and how much of the variation is due to differences in the environments. Nowhere have they slipped into the error of inquiring which is more important, heredity or environment; or of seeking to discover whether heredity or environment determines the development of the individual. For this, as well as for the thoroughness of the investigations, the authors are to be commended. It is not so easy, however, to commend them on their final conclusions and interpretations, one of which, at least, seems to the reviewers to be potentially misleading. But let us first turn to the investigations themselves.

Both the extreme hereditarian and the extreme environmentalist are doomed to disappointment if either is looking for unqualified confirmation of his viewpoint in this volume. Newman, the biologist, Freeman, the psychologist, and Holzinger, the statistician, attempt an evaluation of the relative roles of heredity and environment in the development of certain physical, mental and personality traits, based upon the comparisons of fifty pairs of identical twins reared together, fifty pairs of fraternal twins reared together, and nineteen pairs of identical twins reared apart. The book consists of three parts.

Part I is devoted to a discussion of the biological aspects of twin studies. Literature on twins is briefly reviewed and the chain of evidence for two types of human twins, monozygotic and dizygotic, is summarized. Disadvantages of the fetal-membrane method of diagnosis are discussed, as compared with the similarity method. The following criteria were used by the authors as meeting the requirements of monozygosity: so similar in general appearance as to be mistaken for each other; essentially identical in hair color, texture and form; same eye color and pigment pattern on the iris; same skin complexion (unless one is tanned) and amount and distribution of body down; essentially the same facial features; similarities in dentition; hands and fingers of the same type and proportions; general microscopic character of the friction ridges of fingers and palms essentially the same; and stronger cross resemblance than internal resemblance in most of the details of finger and palm patterns. One can be reasonably sure that the twins investigated by the authors have been correctly diagnosed.

Two prenatal factors are discussed as probable explanations for certain differences occurring in identical twins. The first of these, the fusion of fetal blood vessels between twins and the consequent inequalities of the blood supply, is considered to be largely responsible for quantitative differences not expressed asymmetrically, such as stature, body weight, head length and breadth, and intelligence quotient. The second is the asymmetry mechanism, which is assumed to affect in identical twins primarily those kinds of characters that have an asymmetrical expression in single individuals, such as hand-

*NEWMAN, H. H., F. N. FREEMAN, and K. J. HOLZINGER. 1937. Twins: A Study of Heredity and Environment. 369 pp. Univ. of Chicago Press.

edness, hair whorl, dentition, dermatoglyphics, etc. The senior author believes the reversal or mirror-imaging of such traits in a considerable proportion of identical twins is due to a disturbance in the asymmetry mechanism, induced by the twinning process. In an attempt to show that mirror-imaging in handedness and direction of occipital hair whorl occur with greater frequency in identical than in fraternal twins, fundamentally unsound methods unfortunately are used in the interpretation of the data. Assuming ambidexterity to be an expression of a certain degree of left-handedness, the authors find in an analysis of their own twin data and that of Dahlberg, von Verschuer and Hirsh, a total of 241 pairs of identical twins, that 75 pairs (31%) show some degree of left-handedness in one or both members of the pair, whereas in a total of 274 pairs of fraternal twins only 45 (16%) show some degree of left-handedness. A further comparison is made on the basis of zygotes involved, two for each pair of fraternal twins and one for each pair of identicals, which reduced the percentages of left-handedness in fraternals to 8.2% but leaves identicals still at 31%. One must remember, however, that on the zygotic basis, the average degree of left-handedness per zygote in identical twins is less than in fraternals, because four instead of two hands are involved.

Furthermore, it is not clear why twin pairs in which *both* members are left-handed or *both* ambidextrous should be considered as any more intimately associated with mirror-imaging than those pairs in which both members of the pair are right-handed. The authors regard the asymmetry mechanism as a third factor in producing differences in identical twins, distinct from both heredity and environment.

Identical-Fraternal Comparisons

Part II is a résumé of the studies of fifty pairs of identical twins and fifty pairs of fraternal twins reared together. The two groups of twins were measured and compared for height (both standing and sitting), weight, head length and width, and total ridge count values of fingers. Mental, personality and motor abilities were compared on the basis of test scores on the Binet and Otis intelligence tests, the Stanford Achievement test, and Woodworth-Mathews Emotional Instability test, the Downey Will-Temperament test, and speed of wrist and finger tapping. Fifty-two pairs of like-sexed sibs were compared with the two types of twins for standing height, weight and Binet I.Q. No significant differences were found between the fraternals and the sibs, thus indicating that the twinning process in no way affects normal development in these traits.

Distributions of differences for the various traits in the two types of twins were plotted. The results show that the sharpest contrast between the two types of twins is in the number of finger ridges. In other physical traits the contrasts become less in the following order: height, head length, weight and head width. The contrast in Binet I.Q. is somewhat less than in finger ridges, height, weight or head length, but is sharper than in the Otis I.Q., and the personality and motor tests.

A chapter is devoted to a more refined statistical analysis of the comparisons. The method employed is discussed below; it is sufficient here to agree with the authors that the method is in any case valuable in bringing out *relative* degrees of environmental influences which appear for the several traits measured. Seventy-five to 90% of the intra-pair difference in physical traits is found attributable to nature, whereas 65 to 80% of the difference in the Binet and Otis tests is due to nature, and in the Stanford Achievement tests only 64% is due to nature. Various items of the Stanford Achievement tests show interesting variations. In arithmetic computation the nature factor is responsible for only 12% of the difference, whereas in spelling, nature contributes 53%. An interesting compari-

son of degrees of similarity in handwriting of the two types of twins is discussed.

Identicals Reared Apart

Part III contains complete case studies of nineteen pairs of identicals reared apart, and this section also summarizes and compares the data obtained from all three classes of twins. A rather brief, but intensely interesting chapter is devoted to human interest stories of nine of the separated pairs, as related by the twins. Expenses were paid for transportation of each of the pairs to Chicago for examination. The criteria previously mentioned were employed in diagnosing the twins, and there seems to be no reason for doubting that all of the separated cases are actually monozygotic. In addition to the measurements and tests used in the studies of twins reared together, the separated pairs were given the following mental and educational tests: Thurstone Psychological Examination, International Test, Kent-Rosanoff Free Association Test, and the Pressy Test of attitudes. The twins ranged from eleven to fifty-nine years of age. With the exception of two pairs, all were separated when 18 months or less of age. One pair was separated at 3 years and the other at the age of six. The degree of separation ranged from complete separation over the entire period to a case in which one pair lived only a few miles apart and attended the same high school for three years. Ratings of educational, social and physical environmental differences were made from the case histories by five judges. Fifteen pairs are classed as having had only moderate differences in environment, and four pairs as having had rather extreme differences. Statistical analyses of the data bring out interesting contrasts in estimates as to the proportion of differences attributable to environmental factors, depending upon whether identical twins reared together are compared with fraternal twins reared together, or with identical twins reared apart. By the former comparison, the share of environment in determining weight is .21, whereas by the latter method it is .87. Likewise, for Binet I.Q. the two types of comparisons give .31 and .59; for Otis I.Q., .16 and .64; and for Stanford Achievement, .36 and .87 respectively. These comparisons further indicate that the proportion of difference in the above mentioned traits attributable to environment when identicals reared together are compared with identicals reared apart is approximately the same as that attributable to heredity when identicals reared together are compared with fraternals reared together. As would be expected, finger ridge count, stature and head length appear to be largely governed by heredity, in either type of comparison. On the whole, the data indicate that "physical characteristics are the least affected by the environment, that intelligence is affected more; educational achievement still more; and personality or temperament the most." It is pertinent to observe in this connection that on other grounds our measures of physical traits are the most valid, that the tests of I.Q. and achievement have less validity, and that the validity of personality and temperament tests, such as the Downey Will-Temperament, are highly questionable. Significant correlations were obtained when the estimated amount of difference between the environments was compared with the scores of the separated twins. The correlation between schooling and educational achievement was .91; schooling and intelligence, .46 to .79; and social environment and intelligence, .32 to .53.

Of the four types of conditions which in their various interactions are necessary for an ideal experiment for determining the relative importance of heredity and environment (identical heredities, completely different heredities, identical environments, and absolutely different environments) only the first is attainable. The authors, of course, clearly recognize that fraternal twins have as similar heredity as sibs

and that the differences in the environments of twins reared together and those reared apart are arbitrary. In their conclusions they state: "The analysis indicates that the role of heredity and environment in producing twin differences is a function of the type of environment. Thus, for twins reared together, most of the differences between members of a pair may be due to the nature factor; whereas for twins reared under strikingly different environments, the nurture factors will have a relatively greater influence. It is apparent from several of the types of comparisons made that the relative effect of hereditary and environmental differences is also a function of the type of trait. Any fixed ratio of these two factors for all traits and conditions is thus impossible. . . . From the viewpoint of the educator it is important to note that extreme differences in educational and social environments are accompanied by significant changes in intelligence and educational achievement as measured by our tests."

A fourth type of twin study would be desirable to round out and check the investigations recorded in the book, namely, comparisons of fraternal twins reared apart. Moreover, comparisons of identicals reared apart with fraternals reared apart should give us some clue as to whether or not the environments of identicals reared together is more similar than that of fraternals reared together.

Statistical Methods

Turning to the details of the statistical analysis, the following points deserve especial comment. For a given trait, and for unseparated pairs, there is set up the following function of the identical and fraternal correlations,

$$h^2 = \frac{{}_{i}r - {}_{f}r}{1 - {}_{f}r}.$$

The interpretation of this function is best made in terms of difference-variance, which consists of the average of the squared differences between paired individuals. Through use of the correlation holding in respect to the individuals paired, difference-variance is easily converted into variance in the ordinary sense. Under four assumptions, Holzinger shows that h^2 represents that proportion of the observed fraternal difference-variance which may be ascribed to genetic differences between members of the pairs. Conversely, it is that proportion of the fraternal difference-variance which is left over when prenatal and postnatal environmental factors tending to differentiate the twins have been taken into account.

With two of his assumptions, namely, that the measurements of the trait are reliable and that the range of variation of the trait is the same for identicals as for fraternals, there should be no quarrel, since in any case corrections for departures from these conditions are entirely feasible. The third assumption, that the difference-variance ascribable to environment is the same for fraternals as for identicals, is, in our opinion, clearly hazardous in the case of personality functions. The fourth assumption is that the correlation between genetically caused intra-pair differences and environmentally caused intra-pair differences is negligible. The author states that this correlation will generally be much smaller than the correlation between genotype and environment.

Holzinger points out that he is here attempting to deal not with the environmental or genetic difference-variance of the total population of which the twins are a part, but instead with intra-pair fraternal difference-variance alone. He agrees that this constitutes a limited aspect of the nature-nurture problem. Using the difference between h^2 and 1, however, the investigators find that "about 25 or 30 per cent of the variance in intelligence in fraternal twins reared together may be attributed to environmental influence."

It seems worth while here to compare this approach with one advanced

by a different author* which attempts to take full advantage of the information afforded by the two twin coefficients. In case two further assumptions may be made, that mating is random and that dominance is absent in respect to the trait considered — thus making it possible to assume .5 as the genotypical correlation between the fraternals—, then, as Ignatiev has shown, the genotypical proportion of the total difference-variance of the population of which the twins are a part is determined by the function, $\gamma = 2\,{}_t r - {}_f r$. In harmony with Holzinger, Ignatiev considers the quantity $(1 - {}_t r)$ to be a measure of the difference-variance which may be attributed to intra-familial environmental effects tending to differentiate individuals. Now the difference between the sum of these two quantities and unity, which is $2_f r - {}_t r$, gives us that proportion of the total difference-variance of the population which may be ascribed to "*inter*-familial" environmental differentiating effects.

Though not included at all in the values found for t^2 and h^2, it is the effects of this latter important class of influences which Newman, Freeman, and Holzinger have been able to picture so vividly for us through their study of pairs XI and XVIII, in which one member of each pair happened to be raised in educational and economic circumstances which differed markedly from those for the other member. It is of course just this class of environmental influences which are traditionally pointed out by the so-called environmentalist.

The severest critic could not but praise the candor and the clarity with which the authors have presented the detailed results of their co-ordinated efforts. The intelligence tests used were well chosen considering the date of the inauguration of the project. There will doubtless be some question concerning the way in which the authors handled the matter of I.Q. range. On this point it should be noted that the old Binet did not pretend to include an accurate standardization of range, and that with such cumbersome units as months of mental age to work with it is not surprising that different persons arrive at different methods of presenting such data. However, where differences between twin groups in respect to range of scores render twin correlations noncomparable, it is sounder to use for comparison the intra-pair difference-variance in each group than it is to compare "standard errors of estimate," as the authors do. Or, through the use of the same statistic, in lieu of Tables 88 and 96 there might have been presented the correlation coefficients for the separated twins corrected to the ranges involved in the coefficients for the unseparated twins. The authors exercise caution in interpreting the results they obtained with the invalid Downey Will-Temperament Test; they nevertheless milk this cow very dry.

What is the "Answer"

Taking modifiability as of the very nature of intelligence and accepting without further argument the point that levels of intellectual performance in humans may be raised or lowered by environmental influence, to the reviewers the problem is now that of the extent to which our various environments, as they stand, *are* producing differences ascribable only to non-uniformity in opportunities for development. It is axiomatic, of course, that an approach to uniformity to environment would simply cause to approach 100% the proportion of our difference-variance

*Ignatiev, M. V. 1934. The measurement of genotypical and paratypical influences on continuous characters by means of the twin method. Proc. Maxim Gorky Medico-Biol. Inst., Moscow, pp. 18-32 (in Russian with English summary). Ignatiev does not take account of errors of measurement, but he gives suitable corrections to be applied when degrees of dominance and assortative mating are known and not negligible, or when these influences may not be expected to cancel each other in their effects on the genotypical fraternal correlation.

ascribable to genetic differences. The problem may be viewed thus as a matter of estimating the amount of effective non-uniformity of environment present in our population.

Newman, Freeman, and Holzinger write in summary: "In brief, if the environment differs greatly as compared with heredity, the share of environment in determining traits which are susceptible to environmental influence is large. If, on the other hand, there is large genetic difference and small environmental difference, the share of heredity is relatively large. This is what makes the solution of the question as to the relative share of the two sets of factors indeterminate. We would have to specify what degree of genetic difference is to be compared with what degree of environmental difference."

To us the problem is indeterminate only in so far as the cart has been put before the horse. Populations and their environmental conditions may indeed be expected to differ considerably, and we must therefore specify the population in which we are interested. It is then not a matter of specifying what degrees of genetic and environmental differences are to be compared, but of finding out in fact what proportions of environmental and genetic difference-variance make up the observed difference-variance of the general population considered.

For traits whose mode of inheritance and conditions of mating are known, approaches like those of Ignatiev would seem to render solutions reasonably determinate. However, Newman has raised an important question when he holds that differences in identical twins are predominantly due to prenatal factors. This would mean that the quoted 25 or 30% of fraternal twin difference-variance found for intelligence is in small degree attributable to environmental influences during infancy and youth, but is in large degree due to prenatal influences which are peculiar chiefly to twins. We evidently stand in need of further information on this point, and until we have it, we cannot well be certain of the significance for non-twin individuals of nature-nurture determinations based upon twins.

Reasonable persons will not doubt the authors in their contention that environment *can* produce differences in intelligence greater than those which appear between unseparated fraternal twins. In any case it is clear that these investigators have proved this proposition, although we fail to see how they are thus led to feel sympathy for the very broad dictum that "what heredity can do environment can also do." This conclusion may be misleading when read by the non-biological reader, or even when read by the biologist who is not abreast of modern genetics. It is easy to interpret it as meaning that an adequate environment can make up for an inadequate heredity — an inference which we feel was in no wise intended by the authors.

The book is one which should be read by all students of the nature-nurture problem. While not answering all questions the reader would like to have answered, it will most certainly cause him to appreciate more fully many of the difficulties involved in the problem.

D. C. Rife
Bronson Price
Laurence H. Snyder
The Ohio State University

Twins—a Journal "Godchild"

The studies which are the basis of the book reviewed above had their beginnings in this Journal when Popenoe recorded in 1922 (Vol. 13, No. 2) a case of obviously identical twins reared apart. Dr. H. J. Muller, who was soon to discover the mutational effects of X-rays, obtained the cooperation of these twins to make a detailed study of their physical and mental similarities and differences. This was reported in the Journal in 1925, and this report constitutes case I, in the book under review. The techniques developed by Muller were modified and expanded by Newman in studying the later pairs. Reports on the first ten pairs studied by Newman were published in the Journal between 1928 and 1934. Thus this most important contribution to the nature-nurture problem is one in which members of the A.G.A. may feel a certain pride of publicational god-parenthood. Ed.

THE DOMESTIC ANIMALS OF MONGOLIA

A Review

SHE-YAKS ON THE RANGE

Figure 10

Mongolia is a herdsman's paradise with only one acre in two hundred under cultivation. There are nearly half a million yaks in Mongolia, and about three times as many cattle. A total of over 40,000 yak × cattle hybrids make these bovine mules one of the large hybrid animal industries of the world. The yak is peculiarly adapted to high altitudes and the arctic winters of Central Asia, where it is able to thrive under conditions too severe for cattle. No shelter of any kind is provided for livestock.

THE book* contains ten papers, seven of which summarize the results of an expedition organized by the Academy of Science in 1931. In a short article Prof. Lus gives a sketch of the general plan of the expedition and of the work accomplished. Shulzhenko describes the economics of animal breeding in Mongolia, —which is chiefly range country. Only 39,000 hectares out of a million and a half square kilometers (less than four-tenths of one per cent of the total area) are under the plough. The census of 1930 gives the following numbers for the different kinds of domestic animals: 1,380,600 head of cattle, 449,600 yaks, 40,700 hybrids (cattle × yak), 15,574,400 sheep, 4,075,700 goats, 1,550,400 horses, and 480,600 camels.

Animal husbandry methods are very primitive, being entirely on a pasture basis summer and winter, with constant movement from place to place (nomadism). During the summer the nomads have their pastures near some river or lake; during the winter they migrate on the higher plateaus where water is scarce and the livestock have to quench their thirst with snow. No shelters of any kind are constructed for the livestock. No hay is collected for seasons of scarcity. Losses of large numbers of animals are therefore frequent during the winter when the ground becomes ice-crusted and the animals cannot get the dried grass from beneath the ice ("djoot," as the Mongols call it). All breeds of domestic animals are consequently of a very primitive and unproductive nature, though extremely hardy.

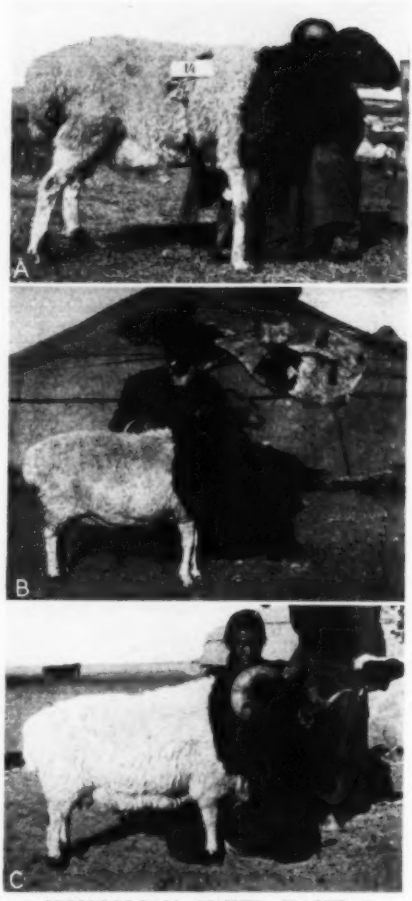
*Lus, J. J., Editor. *Domestic Animals of Mongolia.* Pp. 432. All Russian Academy of Sciences, Moscow. 1936.

Sheep breeding is of the utmost economic importance, as mutton and wool, besides being basic commodities in the nomads' own culture, are exported in considerable quantity. Cattle, yaks, and horses also play a very important part in the economic life of the Mongols. The Mongolian government is endeavoring to improve the productivity of their livestock. Experiments of crossing the coarse wool Mongolian sheep with merino rams are in progress. Imports of bulls of the Simmental breed have also been made. Nevertheless the chief factor for improvement of the Mongol breed must consist of a betterment of the conditions of living (especially during the winter), and selection within the local type. A more detailed review of the several species of domestic animals will be given under separate headings.

Sheep

The sheep of Mongolia were studied by Dr. J. J. Lus, whose aim was to ascertain the diversity of types met with and to evolve a plan for sheep improvement. The Mongolian sheep is quite a distinct fat tailed type with coarse wool. The predominating pattern is white with a colored head, though different types of piebaldness and even occasionally self-colored animals are met with. The live weight averages around 48 kg. for the adult ewes, and about 56 kg. for adult rams. The height at the withers varies between 62 and 68 cm. Thus the Mongolian sheep is a little smaller than the neighboring Kirghiz fat rump sheep, but the body is longer. The fleece is short, with a yield of wool varying from one to two kg. a year. The quality of the wool is finer than that of the fat rump sheep of Khirghizstan.

Prof. Lus believes that the origin of the Mongolian sheep is different from that of the sheep met with in Russian Central Asia, which are of the fat rump type originating from *Ovis ammon* L. It is suggested that the Mongolian sheep must have descended from the fat tailed sheep of Tibet, which is believed to trace to *Ovis Vignei Blyth;* the latter is also held to be the parent of the fine wool sheep (Merino).



MONGOLIAN SHEEP HAVE A CHARACTERISTIC PATTERN

Figure 11

A—Mongolian ram from Central Mongolia (with an apron to prevent the fecundation of ewes). B—A ewe of the Bait variety. Western Mongolia. *C*—A Darkhat ram of Central Mongolia. The Darkhat variety is one of the best sheep varieties in Mongolia. Sheep raising is the most important animal industry in Mongolia.

The author distinguishes eight local sub-varieties of the Mongolian sheep. Those of west Mongolia have more admixture of the blood of the fat rump

sheep and are consequently larger, have a coarser wool and show a greater variability of the fat tail, some forms being intermediate with respect to the fat rump. The Khalhass sheep of central Mongolia is considered to have the best fleece.

The author is inclined to propose selection within the local breeds as the chief method of improvement. Crossbreeding with improved European breeds may be conducted only on experimental farms where some hand feeding must be practiced in winter and where some shelter may be provided for the young lambs and the crossbreds. Some experiments of crossing with improved merinos are already started (1,300 merino rams have been imported). The author thinks that it would be worth while to start an experiment of crossing with the British mutton types such as the Shropshire and the Romney Marsh breed.

J. L. Goroshenko reports that all goats throughout Mongolia belong to one and the same primitive type. The live weight varies from 30 to 41 kg; the height at the withers from 59 to 63 cm. Among Mongolian goats earlessness (of the type described formerly for sheep) is occasionally met with (parallel mutation?). The goats are mostly horned (about 73.4 per cent). The color is variable: gray tones predominate (66.8 per cent). In discussing the origin of the Mongolian goat the author is inclined to the view that all Central Asian goats (Kirghiz, Kazakstan, Tayjikistan, and Mongolia) are of one type, having arisen from hybridization of *Capra prisca* (Adametz) with *Capra falconeri* (Wa) and with *Capra hircus* L. (= *C. aegagrus* Gm.). This conclusion is based on the study of the form of the spiral winding of the horns and their curvature.

Goats are used to furnish milk, meat, and leather. Improvement is advocated only by selection.

Horses

The type of the Mongolian horse is quite distinct. Rumianzef and Voitiatsky find that it differs from the type of the horses of Central Asia thus far studied (the Kirghiz, the Turcoman and others). The Mongolian horse is hardly more than a pony, averaging 126.88 cm. at the withers. It is of a solid and rather compact and heavy body build. Its mane and tail are very abundant. The head tends to be square in outline. The chestnuts are often lacking on the hind feet. Its color is most variable: all the known colors in the horse being met with in the Mongolian pony, but bays and greys are slightly more frequent than others.

The type and the development of the Mongolian horse varies according to the geographical locality. The horse of central Mongolia is the smallest (123 cm.), that of western Mongolia the largest. It is most probable that there is some admixture in Kirghiz blood in the latter.

Horses are used in a great variety of ways by the Mongols. Primarily they are ridden and, in order of importance, they are used as draught animals, for milking and to a limited extent even for meat. A considerable number are exported to China for mule breeding.

In discussing the origin of the Mongolian type the authors reject the possibility of its blood relationship with the wild horse of central Asia (*Equus przewalsky* Pol.) as there are rather essential differences in the build up of the skull (10 skulls of the Mongolian horse have been studied). The authors are inclined to connect the Mongolian horse with the Tarpan, the wild horse of Eastern Europe, which became extinct during the last century.

Some infusion of oriental blood from the Turkoman horse through the Kirghiz may have taken place. In discussing the geographical distribution of the Mongolian type the authors are inclined not only to connect it with the Siberian horse but also with the Russian Viatka, the Estonian Klepper, the Finnish and perhaps even the Norwegian horse.

In recommending methods of improvement the authors are inclined to advocate selection within the local type as the chief method. They think that whereas western Mongolia must aim to produce a better light saddle type, eastern Mongolia should aim to develop a

more compact draught type. With the betterment of the environmental conditions, types of higher culture may be sought for crossing purposes. The authors suggest crossing with the Kuzhetsk horse of Siberia for the improvement of the draught type, and possibly with the Orloff trotter. For the improvement of the saddle horse, the horse of the Don may be recommended.

Cattle, Yaks, and Hybrids

A study of the morphological types as well as of the craniological characteristics of the Mongolian cattle leads N. N. Kolesnik to the following conclusions:

(1) The Mongolian cattle forms, together with the Kalmuck, the Kirgniz and the Yakut breeds, quite a distinct type, differing in its craniological and other morphological characteristics both from the European cattle (*Bos primigenius* and *B. brachyceros*) and from the forms of southern Asia.

(2) All the above-mentioned breeds are the offspring of a subvariety of the wild bovidae of Asia that has been domesticated in the south or southwest of Mongolia.

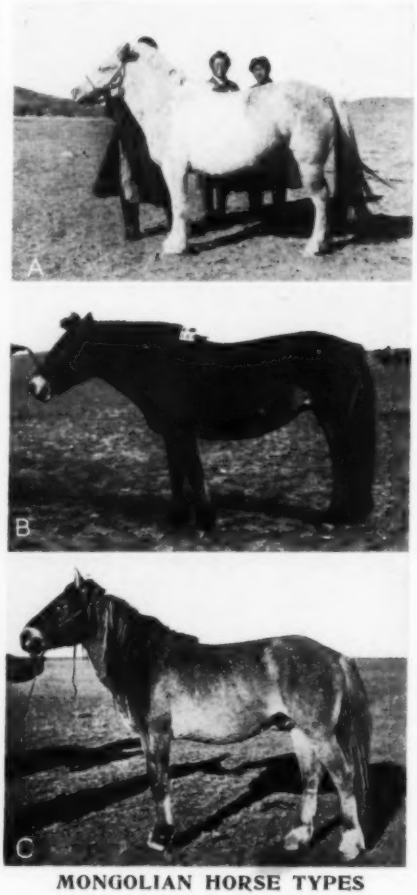
(3) Cattle are unevenly distributed over Mongolia. The northeastern part is richer in cattle than the southern and southwestern parts.

(4) The Mongolian cattle is of a primitive type without signs of specialization. Its live weight is low (about 275 kg.).

(5) A rather wide range of variation is present with respect to the dimensions and color and markings, which has led to the formation of a variety of local types.

(6) The primitive conditions under which the cattle are held lead to rather large losses in severe winters. This is a serious drawback to ascertaining the real productive ability of the cattle and for their improvement.

(7) Improvement of these conditions (building of cattle sheds or barns, winter feeding with hay and concentrates, better feeding of calves) are essential prerequisites to further improvement by selection and crossing.



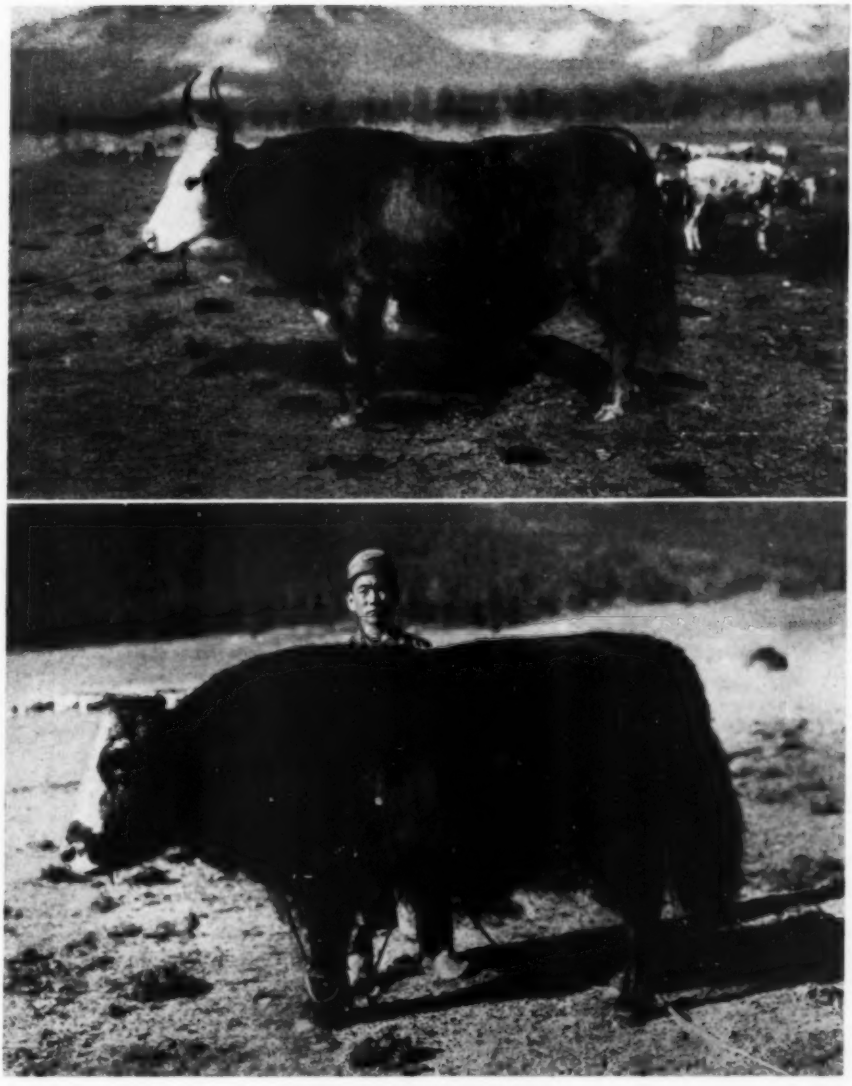
MONGOLIAN HORSE TYPES

Figure 12

A—A light-yellowish-wild piebald mare from the Delherkandaj District s. East Mongolia. *B*—A bay Mongolian mare from the Ulzyn District of Eact Mongolia. *C*—A stallion from Western Mongolia. The authors believe that the Mongolian horse descends from the extinct Tarpan and other European species rather than from Przewalsky's horse the wild type in Asia.

(8) The author advises that the experiment be undertaken of crossing the Mongolian cattle with the Simmental and Brown Swiss breeds.

The yak was studied by Dr. J. J. Lus, who made detailed measurements of 89 Mongolian she-yaks and some 34 hybrids (yak-cattle), 15 measurements be-



YAK-CATTLE HYBRIDS

Figure 13

Above are shown two female first-generation yak × cattle hybrids. In this cross the females are fertile while the males are sterile. The hybrid vigor exhibited by this cross is evident in an increase of about one-fifth in the live weight of the hybrids as compared with the heavier parent (cattle). Some vigor is shown in the backcross of the female hybrids to either parent species, but later generations are considered to be of no economic value.

ing taken on the live animal. We will only point to the height of the withers, which averaged 109 cm. No marked differences could be ascertained between the yaks of Mongolia and those of Kirghizia and Oirotia, except that the per cent of polled animals is highest in Mongolia (88.5 per cent among females). This must be wholly attributed to artificial selection as the Mongols have a strong predelection for polled animals. The author did not observe any horned bulls, all the horned bulls being castrated. The hybrid of the first generation with cattle shows a marked heterosis. All his dimensions are larger than those of either parental form. The live weight of the hybrid is about 18 per cent greater than that of cattle. The female hybrids of the first generation may be backcrossed to members of either parent breed. The male hybrids are sterile. Some heterosis is yet present in the backcross (¾ and ¼ blood) animals. Later generations of the hybrids are considered to be quite unproductive and are eliminated.

In color the domestic yak is rather variable. Only about 20 per cent are of solid color—80 per cent show a more or less large development of white markings which may end in a practically pure white with a few colored specks. A sort of roaning giving a blue tint to the animals is met with in 21.5 per cent of cases Of the types of white markings, two independent series may be mentioned—white markings on the head, tail, feet, inguinal spot, and the "color sided" type of piebaldness described also in cattle (parallel mutation?). The wild type of pigmentation (agouti) is met with, though animals of pure black and pure brown are rather more frequent.

F. Denisov and S. Ushakov report on yak breeding in the Altai Mountains. The yak is an animal indigenous to rather high altitudes, and is well adapted to graze on steep mountain slopes unaccessible to cattle. It is an excellent pack animal for mountain travel. But the domestic yak is of small stature, and gives a rather small carcass of low quality meat. Its milk yield is low, though the fat content of the milk is high (6.34 per cent). The more vigorous yak-cattle hybrids give a large carcass of better beef. The milk yield of the female hybrids is higher than that of the pure bred yak, and the fat per cent intermediate.

The type of the yak from the Altai mountains does not differ materially from that of the Mongolian yak studied by Lus. (Measurements on 49 female yaks.) Hybridization of the yak with cattle in order to make use of the hybrid vigor of the first generation is most advisable. The question of using the yak in crosses to increase the fat yield of ordinary cattle is a rather complex question that can not as yet be solved; further experiments are needed.

The Buriat-Mongol sheep is nearly related to that of Mongolia; it is the same fat tail coarse wool type of sheep, white in color with characteristic markings. In order to improve the quality of its fleece crossbreeding experiments have been conducted with the merino. Diomidova and Muruev reported a marked improvement in the character of the fleece, and in the quantity of the wool (2.38-3.3 kg). An increase in the early maturity of the animal and in the number of twins has also been attained. The live weight has slightly decreased. A great variety of piebaldness appeared in the F_1 generation.

The volume concludes with a discussion by Professor N. N. Poppe on the origin of animal breeding by the Mongols. The paper is a philological and historical study that leads the author to the conclusion that in the Thirteenth Century, when the Mongols united to form the empire of Chingiskhan they already had a well developed animal breeding of a nomadic type. Most of the tribes were animal breeders from the beginning of the Christian era, and perhaps even earlier. At that time they had rather near connections with the tribes of the Turcks and of the Mandjuro-tunguss. The roots of the Mongolian animal breeding may have extended into the still more ancient west Siberian culture that has been dated as early as three or four thousand years B. C.

D. Kislovsky

BASTARDS OF THE WORLD UNITE!

A Review

ORGANIZATION is the catchword of the day and collective action is the current cure-all. Humanity has been cut in almost every imaginable plane and we are familiar with organizations directed against races as well as with those working for race preservation and aggrandizement. It might have been expected that with these race collectives the farthest depths of silliness in human agglutinations would have been plumbed but such it seems is not the case. Mr. Cedric Dover, himself an Eurasian, has discovered a choice lot of unorganized humanity in the race hybrids of this world and these he urges to unite on the grounds that they have one thing in common—they are all bastards.*

Now no one attempts to found large and prosperous organizations by pointing out to prospective members that they are so physically weak and so mentally defective that their only hope for survival lies in union. Recruits come more willingly to organizations founded on the superiorities, either real or imaginary, of their members.

Mr. Cedric Dover has learned that simple lesson and sets out not merely to condone and defend the bastards of the world but to extoll them. First he shows how all those who react unfavorably to mongrel humans are actuated either by ignorance or by prejudice, usually base. Then he shows that the populations of the world are so thoroughly mixed, as the result of migrations, that after all we are each and everyone bastards. He even gives credence to the myth of a pre-Columbian influx of near Easterners into Central America.

One would suppose, having made the comprehensive point that we are all mongrels, anything further in the support of hybrids would be superfluous, but the author proceeds and, in proceeding, proves one contention of some of the antagonists of race hybrids — namely that such hybrids embrace the bad qualities of both races. For in Mr. Dover's work we find in full flower the exuberant verbal nebulosity characteristic of East Indian philosophy combined with the lack of logic which is one of the charming features of some Irish literature.

Having disposed of the races of mankind as being imaginary groups existing only in the prejudiced minds of dominant people, and thereby proving there is no distinct group of race hybrids, the author goes on to show how bastards everywhere not only think alike but are indistinguishable physically. He then devotes a chapter to confounding those who have expressed themselves as opposed to racial blending. Head cracking in this field is easy, for the blah emitted by authority *A* can be nicely controverted by that emanating from authority *B*, and Mr. Dover enters into the fun with great gusto and to much effect. In print, by judicious quotation, one savant looks very much like another, giving the lay reader no choice but to assign each equal weight.

When the thesis, that bastards as a group are no worse than other humans, has been proven to the author's satisfaction he undertakes to show that indeed they are superior to the pure breds. For this purpose he limits himself to the achievements of what might be called layman's bastards — persons whom everyone would recognize as race hybrids though not by any means hybrids of the first generation. Some of his examples would be technically described as first or second backcrosses. With these the author has not done as

*DOVER, CEDRIC. Half Caste. 10S 6d. Martin Secker & Warburg, Ltd., London, 1937.

well as he might and much of the evidence adduced for bastard superiority will impress the reader as puerile. The poetry of unsung Anglo-Indians, quoted at length, will not go far toward persuading any one that more race hybridization would be a fine thing for poetry.

Unquestionably the book is inspired by the race betterment efforts of present-day Germany and it should be viewed as an example of counter propaganda—a sort of return swing of the pendulum. No doubt that is the way Prof. Hogben viewed it when he undertook to give it dignity with a very excellent preface on prejudices.

The whole subject of the races of man has been confounded by the looseness of language no less than by the looseness of man. Strictly speaking pure races of man are non-existent. Anthropologist, however, have been able to classify man into racial groups and this classification, though admittedly inexact, is useful.

It is true that countless numbers of individuals are racially so mixed that disentangling their web of heredity is an impossibility. Our inability to place racially thousands of individuals should not be allowed to obscure the fact of group or race distinctions in man any more than the existence of thousands of mongrel dogs should lead us to deny the existence of breeds of dogs. That the races of man like the breeds of dogs have precipitated from populations does not make them any the less real.

Isolation leads to racial differentiation no less in man than in other animals. That racial blends are found where racial ranges overlap does not mean that races of man do not exist, but on the contrary shows that they do. It is true that geographic isolation is disappearing rapidly but there remains the almost equally effective isolation of numbers. Four hundred million Chinese can not be racially altered by a few hundred thousand crossings.

Although racial admixtures are probably more numerous now than in times past there is no immediate likelihood that the races of man will be blended into a uniform whole. That the major races are secure does not mean that race hybrids do not constitute an increasingly serious problem in many countries.

Our reactions to racial hybridization are influenced largely if not wholly by prejudice and superstition though it should be recognized that even prejudices and superstitions may have respectable origins. The superstitious fellow who avoids walking under ladders is somewhat less likely to suffer from head injuries than is his emancipated neighbor.

Admitting the actual existence of race mongrels in man and hence of races, it follows that there are recognizable group differences in humans. No quantity of published refutations can destroy the fact of race. Whether some races are superior to others or whether some excel in one thing, others in another, becomes a question of definitions. Probably each race has superior qualities when viewed within the restricted frame to which it is adapted.

After all, the best evidence for achievement and, therefore, on the whole of innate ability is the position occupied by the races today. This is the time in which we are interested in race accomplishment and the results to be expected from hybridization. That a given race once held a high position in world civilization is no guarantee that the ability to reach the pinnacle again lies latent within the germ plasm or that it would be brought into expression by promiscuous hybridization.

Nothing much is to be gained from the standpoint of present-day reaction to race crossing by stating that the Egyptians had a flourishing civilization of high cultural elements 3,000 years ago and that this proves colored peoples can establish superior civilizations. There is very good evidence that the Egyptian was not a civilization of colored people but whether it was or

not has little bearing on the question of today which is what can be expected genetically from hybrids between negroes and whites. The sociological problems are relatively minor, being transitory, but the genetic consequences are more lasting.

Although specific genetic results to be expected from race crosses can not be accurately foretold it is common genetic experience that one result of hybridization is an increased variability in the generations succeeding the first cross.

If we were confronted with inbred populations having a restricted variability and saw the need of a more fluid material from which to derive desirable characters the suggestion to increase race crossing would be sensible. However, as everyone readily admits, and indeed as Mr. Cedric Dover so eloquently claims, the races of man are not pure and neither do they lack variability. Within any race the variability is so great that given adequate control and continuity of effort any modern breeder could plan a breeding system which, within a few generations, could make measurable progress in shifting the race backward or forward physically or mentally.

Under the circumstances and quite apart from whether or not the German effort for race improvement agrees or conflicts with our prejudices it is just the sort of system, under the limitation of human breeding, that breeders would establish to fix the characteristics chosen as desirable.

We may believe, as many authorities do, that the German ideal is poorly chosen or that proscription of people of Semetic ancestry is foolish but that is a choice for the Germans. It may well be that the German people regard the melting pot system of breeding now functioning in this country and in the British colonies as wholly undesirable. Time will decide which system results in the highest achievements and to this decision the bastards of the world will make their contribution whether they are organized or untrammeled but there is nothing in the science of genetics that justifies a campaign to stimulate race crossing.

J. H. Kempton

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Brobdingnagian Botanical Boondoggling

THE fourth session of the Lenin Academy of Agricultural Sciences, held in Moscow at the end of 1936, witnessed a determined campaign against genetics as the main basis of scientific plant breeding.[1] It is only now, however, that detailed reports of some of the speeches made at the session are available, while further light is thrown upon the controversy by recent Soviet publications.

The attack was opened by a group of plant-breeding experts headed by T. D. Lysenko, a member of the Odessa Institute for Selection and Genetics. The main ideas of Lysenko do not appear to have been published in a scientific form, but they are expressed in a popular pamphlet[2] and in his speech at the session of the Academy of Agricultural Sciences.[3] They are based on no lesser, and no later, authority than that of Charles Darwin, whose teachings according to Lysenko "were unable to blossom out properly in bourgeois countries. The best Darwinists in capitalistic countries, as for example Burbank in America, as well as our revolutionaries-biologists K. A. Timiriazev and I. V. Michurin in the Czar's Russia, were lone fighters." The works and theories of de Vries, Johannsen, Bateson, Morgan, are dismissed on the strength of a few quotations from their writings, suggesting their critical attitude to some of Darwin's ideas, all of which are held by Lysenko to be the last word in biology.

The actual controversy is centered around two points of practical plant breeding. One concerns the problem of crossing and selection of self-fertilizing pure line plants. According to Lysenko, pure lines if cultivated for a long time are liable to degeneration. This can be prevented, and the line even improved, by artificial cross-fertilization within the variety. "Small field experiments" made at Odessa with some varieties of wheat have shown an increase in the yield from cross-fertilized seeds, and this was taken to be sufficient to consider the method ready for immediate introduction into practice. About 10,000 farmers on 2,000 col-

lective farms were instructed to sterilize wheat plants by cutting stamens to prevent self-fertilization. As a result, 500-1,000 gm. of cross-fertilized seeds were obtained on each farm. "If it happens that the seeds from intra-varietal crossing should be of higher quality, should produce plants with greater yield . . . . there will be no obstacle to a rapid transformation of a kilogram of seeds on each farm into tens of tons." Since Lysenko is also practically certain (although without apparent data) that the improved plants will be more resistant to winter frosts, he urged the Academy to pay serious attention to the question of the immediate necessity of introducing the method of cross-fertilization on "at least 50-70 thousands of collective farms."

It does not appear to be safe to criticize such enthusiastic plans, containing a promise of enormous and immediate progress towards the fulfilment of Stalin's recent order for increased agricultural production. N. I. Vavilov,[4] in his reply to Lysenko, merely pointed out that many pure varieties of wheat, barley, etc., have existed without any "degeneration" for centuries, and there is no need to seek to improve them by intra-varietal cross-fertilization. Even if such crossing should produce an improvement (due to heterosis), it remains to be shown that the improvement will be lasting, since usually heterosis disappears in a few generations. G. Meister,[5] who summed up the discussion, very cautiously suggested that it would be premature to develop extensive practical programmes while the method is still being studied experimentally.

While this first point of the discussion was mainly concerned with a practical problem, the second presented a clash between two almost diametrically opposed fundamental conceptions of biology. The discussion developed round Lysenko's forceful statements that the external conditions under which a plant develops have a profound effect not only on the somatic, but also on the sex cells. Therefore, responses of the constitution of an individual plant to its environmental conditions are inheritable, contrary to the views of "bourgeois" geneticists. This theory is based on three incomplete years of experiments with the vernalization of winter wheat and rye; none of these experiments was carried beyond the fourth generation and the results do not appear fully conclusive.[2, 5] Nevertheless, Lysenko claims that the possibility of "changing the nature of plants" has been definitely proved, and promises in the near future to develop new varieties of winter wheat with increased cold-hardiness, of cotton requiring less heat for its growth, etc.

On the face of it, Lysenko's theory is nothing but Lamarckism in its simplest form, and this was pointed out by several speakers. Such accusations of being unfaithful to Darwinism appear, under Soviet conditions, to be tantamount to charges of high treason. Lysenko, therefore, had to insist that his theory is nothing but a development of most orthodox Darwinian views. His defense is worth quoting, since it provides a typical example of methods of discussion adopted by some Soviet scientific investigators: ". . . no work can possibly produce positive results if it starts on the basis of Lamarckism. If, by suitable breeding of plants, we have already succeeded in altering their hereditary nature in the desired direction, this alone proved that we are not Lamarckists. . . ." Lysenko insists further that he is not against the science of genetics, but "genetics as one of the most important sections of agro-biological science must be . . . remade in our Soviet way, without accepting many anti-Darwinian tendencies of fundamental genetic conceptions."

The problem of the inheritance of acquired characters has such an extensive literature and is still so far from its solution, that recent Russian work on vernalization and allied phenomena should be regarded merely as providing additional experimental data on the subject. Some of the results may be suggestive, but they certainly do not in any way justify Lysenko's assertions that the secret of "changing the nature of plants" is now discovered. These assertions would not be worth recording, were it not for the fact that they led, not to a healthy discussion, but to unscrupulous attacks on the large Russian school of geneticists deservedly appreciated by biologists in other countries. It is true that Lysenko and his colleagues veiled their attacks, for example, on Vavilov, by professing profound respect for his work; but at the same time they lost no opportunity for stressing what they consider to be anti-Darwinian tendencies in his ideas. In a country where Darwinism—as interpreted by Engels and Lenin—constitutes the ideological basis of official philosophy, arguments of this kind savour of denouncing an enemy of the State. Some practical effects of these accusations were pointed out by Meister[5], who said that certain Soviet editors already refuse to publish articles dealing with genetics, which appear to them bordering on counter-revolution. It is also perhaps not a mere coincidence that the International Genetical Congress, which should have been held in Moscow this summer, has been postponed.

On the whole, the discussions, which must have stirred very deeply all biological workers in the Soviet Union, appear to be of very limited theoretical interest. They are, however, of outstanding significance in revealing the atmosphere in which scientific investigators in totalitarian countries have to live and work.—*Nature.*

[1] *Nature*, 139:185 (Jan. 30, 1937).
[2] "Changing the Nature of Plants" (in Russian). Pp. 46+10 figs. (Moscow, 1937.)
[3] *Pod Znamenem Marxisma*, 2:96-118 (1937).
[4] *Front Nauki i Techniki*, 2:54-61 (1937).
[5] *Front Nauki i Techniki*, 2:62-80 (1937).

AN INTERSPECIFIC HIBISCUS HYBRID

Between *H. ficulneus* and *H. esculentus*

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Institute of Agricultural Research, Benares Hindu University, India

THE genus Hibiscus makes important contributions to the economic products of India. Some of the species are grown as fibre crops,—others as vegetables and as medicinal plants. Owing to its great economic importance, classification of some of the species (*H. cannabinus* and *H. sabdariffa*) was undertaken by Howard and Howard* as early as 1911.

In spite of the presence of a number of species, most of which are cultivated, there is no published record as to their intercrossability. From the systematic standpoint the determination of interspecific crossability is important as it throws interesting light on the affinity existing between the different species. With this aim in view a number of species of *Hibiscus* were grown and crossed with one another. Of the several crosses made, hybridization between *H. esculentus* and *H. ficulneus* (local name, Dula) was alone found to be successful.

In the experiment a long green variety of *H. esculentus* was used as the female parent. The emasculation was performed the previous evening and the pollination made the next morning. A dozen such crosses were made and all of them were successful. In fact fertilization was as normal as in the case of self pollination of *H. esculentus*. The seeds were collected separately and sown in the Kharif season (June-Oct.) of 1936. The germination process of the F_1 seeds was quite normal.

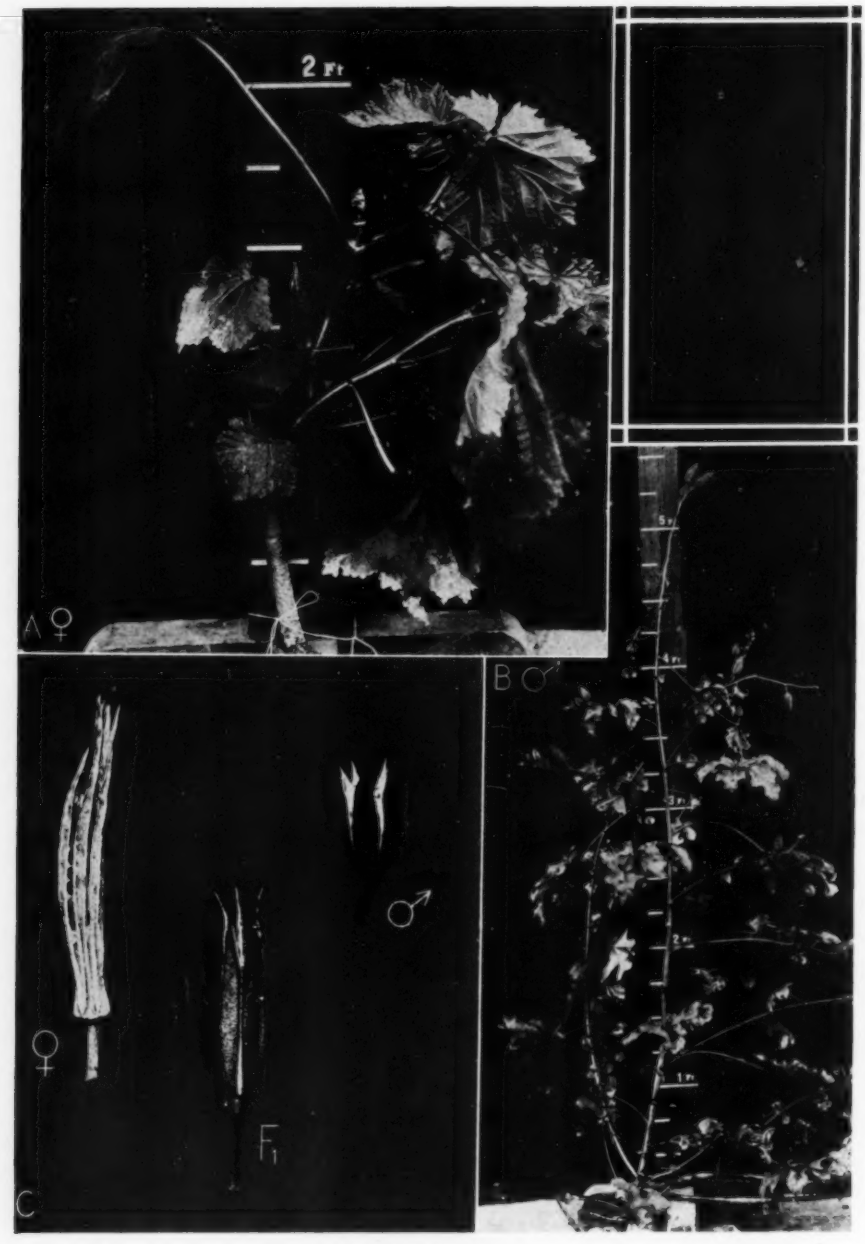
In the following table are given only those characters in which the two parents differ along with a description of

MANY STERILE FRUITS

Figure 14

Stalk of Hibiscus species hybrid showing development of a fruit at the axil of every leaf. Since these fruits contain no seeds the fecundity of the hybrid far exceeds its fertility.

*Howard, A., and Howard, G. L. C. Studies in Indian Fibre Plants. No. 2.—On some new varieties of *Hibiscus cannabinus L.* and *Hibiscus sabdariffa L.* Memoirs of the Dept. of Agr. in India (Botanical Series), IV, 1911.



PARENT SPECIES

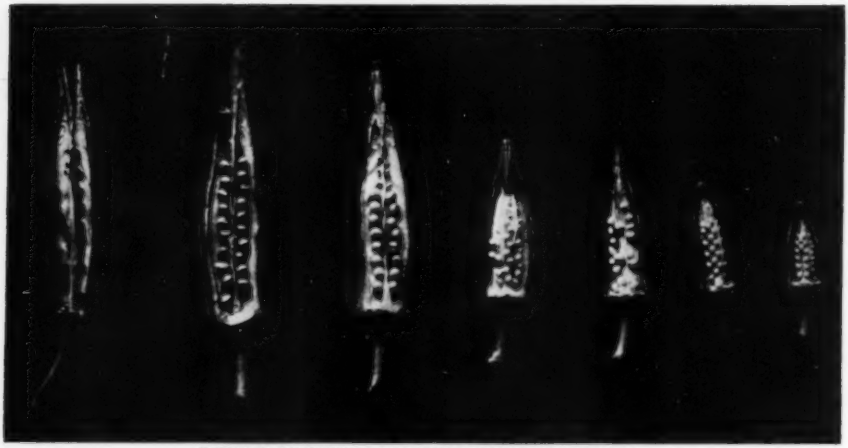
Figure 15

A—The female parent, *Hibiscus esculentus*, is a variety of common Okra or "lady's finger" used as a summer vegetable, and grows less than two feet tall. *B*—The male parent, *Hibiscus ficulneus*, is an Indian species used in the refining of sugar by indigenous methods. The first generation hybrid, between these two forms is shown on the following page. *C*—Shows the ripe seed pods of the parents and the hybrid. Note variations in extent of dehiscence.

MARKED VIGOR OF FIRST GENERATION HYBRID

Figure 16

While one parent grows about two feet tall and the other reaches a height of six feet, the hybrid stands nine feet high and has proportionately vigorous branches. An attempt is being made to cross the hybrid back on to the parent species in the hope that by the use of hybrid pollen some fertility may be obtained in the backcross.



DEVELOPMENT OF THE HYBRID FRUIT

Figure 17

During the early stages of development formation of fruit appears to be normal. Up to quite a late stage no marked evidence of abnormality appears. However, in the ripe fruit (left) the seeds are all shriveled and have no viable embryos. An attempt is being made to determine at what stage of development the embryo ceases its growth.

characters appearing in the F_1 hybrid. Other characters such as leaf apex, flower color, number of fruit ribs, etc., are more or less similar in both the parents and the hybrids, and are therefore purposely deleted.

TABLE I. The contrasting characters of the two parents and hybrid.

Characters	*H. esculentus*	*H. ficulneus*	F_1
1. Growing season	July-September	July-December	July-December
2. Plant height	23″±0.97 (Figure 15)	66″±1.56 (Figure 15)	112″±2.48 (Figure 16)
3. Date of first flowering	26th August	10th November	7th October
4. Number of branches	3.1±0.20	12.0±0.44	21.5±0.59
5. Angle of branching	40°-45°	45° upper branches and 80°-90° lower branches	45° upper branches and 70°-85° lower branches
6. Hairs	Soft, thinly distributed	Short, thick prickly, densely distributed	Short, thick prickly, densely distributed
7. Color of stem	Light green with slight tinge of pink in the terminal portions	Pink, dark pink in the terminal portions	Green, tinged with pink, terminal portions pink
8. Color of leaf	Light green	Deep green	Deep green
9. Stipules	One pair	One pair	Two pairs
10. Epicalyx	Needle like, 8-10 in number	1-1½″x½″ 4 in number	¾″-1″x¼″-½″ 6-8 in number
11. Anthers	Closely set on the staminal column	Closely set on the staminal column	Sparsely set on the staminal column
12. Stigma	Very broad, dark pink, lobes 5-10 closely set on each other	5 lobed distinctly separate and radiating, pink	5 lobed, lobes compact, pink
13. Fertility	Fertile	Fertile	Sterile
14. Fruit length	5.4″±0.13″	2.0″±0.07″	3.4″±0.11″
15. Dehiscence (Figure 15C)	Does not split open completely	Splits open completely	Splits open half way from the tip

The most striking feature of the F_1 plants is their hybrid vigor and sterility. After fertilization the fruits develop normally and attain their maximum size, but fail to produce any seed. In order to trace the seed development process a number of fruits were split open at different stages of growth. All seeds were found to be plump up to a length of 3-4 cms., but in fruits longer than that the proportion of plump seeds to shrivelled ones decreased and finally all of them dried up (Figure 17). The plump seeds of larger fruits when cut open indicate the absence of embryo.

The relationship between the parents and hybrid is summarized as follows:

A. Characters new in the hybrid.
   1. Increased height, branching (Figure 15-16) and number of fruits borne (Figure 14)
   2. Presence of two pairs of stipules
   3. Sterility

B. Characters intermediate
   1. Stem color
   2. Number and size of epicalyx
   3. Size of the fruit
   4. Dehiscence of the fruit (Figure 15*C*)
   5. Time of flowering

C. Characters like the parent *H. esculentus*
   1. Compact stigma head.

The rest of the characters are like that of the parent *H. ficulneus*. The results of back-crossing will be published in a later publication along with the observations on the possible physiological and cytological causes of sterility for which investigations are in progress.

FOUNDATIONS OF EUGENICS

HERMANN MUCKERMANN is a versatile German cleric and physician who publishes a eugenic journal, "Das Kommende Geschlecht," and has written numerous volumes on the family, marriage, and the relation of religion to eugenics, genetics, and evolution. In 1914 he published "Eugenik," a textbook of eugenics. His latest volume, "Vererbung und Entwicklung,"* is an attempt to set forth the knowledge of heredity, individual development, and evolution, upon which eugenics should be founded. The book is divided into three sections: the first deals with the cell, reproduction, and individual development; the second with general genetics and evolution; the third with heredity, racial differences, and evolution in man.

Although the publisher states that more than a third of a million copies of Muckermann's books have been printed, this one is neither oversimplified cheap popular science nor propaganda. Pertinent subjects are fully presented regardless of their difficulty or technicality. In particular, the *methods* of investigation employed in each field are emphasized, and their value and limitations are judiciously appraised. Eugenics based on such a presentation should be sound.

Unfortunately, however, some of the sections most directly related to eugenics depart from the critical and cautious tone that characterizes most of the more fundamental parts of the book. For example, in the discussion of human races, after critically examining the concept and stating fairly its complexities and difficulties, the author proceeds to set forth that *nevertheless* certain general conclusions can be drawn. *Why* they can nevertheless be drawn is not discussed, and the presentation thenceforth ceases to be critical, though it remains moderate.

Even in the presentation of the more fundamental subjects, the material is sometimes so out of date as to lead to conclusions untenable in the light of later knowledge. Thus, in the section on individual development, Muckermann's account reaches its climax in the work of Driesch which is the basis for his own profession of vitalistic faith. The work of his eminent countrymen, Vogt and Spemann, is not mentioned.

Aside from such shortcomings, the book is good. It is well organized, clearly and interestingly written, and generally readable.

T. M. SONNEBORN.

*MUCKERMANN, HERMANN. *Vererbung und Entwicklung.* Ferd. Dümmlers Verlag. Berlin und Bonn, 1937. xii+213 pp. 94 figures. Index. RM. 5.85 domestic; 4.40 foreign.

INOCULATED SEEDLINGS

Figure 18

A shows tobacco seedlings five days after inoculation with mosaic virus. Inoculation was done about ten days after the seedlings were transplanted from the seed bed. *B* shows a flat of seedlings one week after inoculation. At about this stage differences between susceptible and resistant plants begin to be evident. *C* shows the difference in reaction of susceptible and resistant seedlings. The two rows of seedlings on the left are from a susceptible line. The four rows on the right are from a resistant strain. The dwarfing effect of the mosaic infection is evident even at this early stage of growth.

INHERITANCE IN NICOTIANA

III. A Study of the Character for Mosaic Resistance in *Nicotiana tabacum* L.*

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IN 1935 the writer[3] gave an account of infection studies in a resistant tobacco in relation to the virus of the tobacco mosaic.† The resistant tobacco concerned, the variety Ambalema reported by the writer and Roque[4] in 1934, is not a high quality tobacco in Puerto Rico.

Upon discovery of the mosaic resistance exhibited by this important tobacco from northern South America, it was considered desirable to initiate a series of studies directed at the development of commercial strains of tobacco combining the mosaic resistance of Ambalema and the good smoking qualities of other known varieties. The project required, however, that the genetic behavior of the resistance character be known in order to expedite the isolation of resistant lines.

Crosses were begun in the growing season of 1929-30 in Puerto Rico, at the Insular Experiment Station, and continued at the University of Cornell, Ithaca, N. Y., in 1932, and at the University of Wisconsin, Madison, Wis., in 1932 and 1933. The study was completed at the Insular Forestry Station.

Materials and Methods

The variety Turkish (Samsun) (*T*) with petiolate leaves and very susceptible to mosaic, was used in many of the crosses employed for the study of inheritance of the resistance character. This is the same strain as used in the study of the *yellow* and *glaucous* characters reported in another paper[2].

Other susceptible varieties used in the crosses were the White Virginia No. 9 (*Wh. V.*), a native tobacco, and No. 144-9-1, a Phytophthora resistant line isolated from the cross *Cuban* × *Turkish*.

It was evident that the variety Ambalema (*Am*) was not uniform for visible characters. Therefore, several plants were used in the crosses and the resulting progenies were studied separately.

The mosaic-resistant lines 243-7-5-3, 243-7-5-15, 271-1-11 and 271-1-18, isolated from the cross *Ambalema* × *Turkish*, were used in crosses for the purpose of developing commercial strains of tobacco resistant to mosaic. Their progenies were also studied genetically.

Direct and reciprocal crosses were made. The F_1 generation of these and some of the F_2 selections were backcrossed to Ambalema. In backcrossing, one of the flower branches was bagged separately from the rest of the head. In this way backcross and either F_2 or F_3 progenies had the mother parent in common.

Selections in the second generation were made at random in the case of the susceptible plants. Sixty susceptible and four resistant plants were selected in the F_2 generation of *Am* × *T*.

Seed sowing was made from single capsules. Flats of the ordinary size were filled with a good compost and sterilized with steam or formaldehyde. A flat was used for each progeny. The young seedlings were kept in the greenhouse, under sash or under cheesecloth tents. While

* Contribution No. 1. Tobacco Institute of Puerto Rico.

† The term "tobacco mosaic" as employed here refers to the ordinary tobacco mosaic and "mosaic virus" means the virus of the ordinary tobacco mosaic (Johnson's Virus No. 1).

still small the seedlings were transplanted into flats, greenhouse benches or beds, at 2-4 inches apart and inoculated with extracts from infected susceptible tobacco plants within ten days after transplanting. (See Figures 18-19.) The mosaic virus used was derived from the tobacco mosaic virus heated to 85-86° C. for ten minutes. This was necessary because a mottle ordinarily found associated with the former infects and causes symptoms in tobacco resistant to mosaic. The mottle virus is killed or inactivated at temperatures lower than 85° C. The rubbing method described by Holmes[1] was used in all inoculations in greenhouse or field.

Ten to fourteen days after inoculation, all seedlings displaying the mosaic symptoms were pulled and rejected, while those seedlings with mild or no symptoms were reinoculated with the mosaic virus. (See Figure 20.) They were retained over a long period, by transplanting into separate beds. Final check on resistance was made by extracting the juice of the individual plants and inoculating it into F_1 plants of the cross *N. tabacum* (Ceniza) × *N. glutinosa*. In this hybrid even a very low concentration of the virus is detected. Local lesions are produced on the inoculated leaves. Symptomless plants proving to have been infected, and those showing very mild symptoms, were considered as resistant.

Another method employed was planting the progenies in the field and inoculating therein four weeks after transplanting. This method was used only in a few F_2 and F_3 progenies in Ithaca, N. Y., and Madison, Wis.

The inoculated susceptible plants used as source of inoculum were kept isolated from the rest, in glass cages or inside compartments lined with cheese-cloth.

The number of plants per progeny varied, being larger for the F_2 and backcross. In the F_3, small numbers in the neighborhood of 150 were first inoculated; but if segregation occurred, seed was resown and a larger population (300) was inoculated.

The results were tabulated in the customary manner and the data studied statistically. Odds lower than 31.36 to 1 were not considered significant.

In determining the relative resistance of plants the same method was employed as described in another paper[3], i.e., the number of local lesions per every 10 sq. cm. of leaf surface produced by the extract from the infected plant on *N. glutinosa, N. repanda* or *N. tabacum* (Ceniza) × *N. glutinosa.*

Experimental Results

The F_1 generation. The F_1 generation of the direct and reciprocal cross *Ambalema (Am)* × *Turkish (T)* proved to be as susceptible as the susceptible Turkish parent. This susceptibility to mosaic is dominant over resistance.

A comparison was made between the resistance of the F_1, *Am* × *T*, and the susceptible Turkish, using as the measure of difference[3] the number of lesions produced on *N. tabacum* (Cen) × *N. glutinosa* by the extracted juices.

The following figures from ten determinations show that the first generation of the direct cross is as susceptible as the susceptible parent:

Suscept	Mean of 10 determinations. Lesions per 10 sq. cm.	P. E.	D/P. E.
Am × T. F_1 ..	102.208	± 4.880	
Turkish (T) ..	96.98	± 2.111	
D	5.228	± 5.317	0.98

The difference is clearly within the range admittedly due to experimental error.

The second generation. In order to determine quantitatively the segregation of susceptibility and resistance to mosaic, six progenies of *Am* × *T*; four of *T* × *Am*; three of *Wh. V.* × *243-7-5-15* (progeny 690); and one each of *271-1-18* × *144-9-1* (progeny 713), *243-7-5-3* ×*144-9-1* (progeny 716), and *Wh. V.* × *271-1-11* (progeny 685), were inoculated in the seedling stage. The results are given in Table I.

An examination of the results suggested a relation of approximately 15 susceptible to one resistant plant. The hy-

SUSCEPTIBILITY OF FIRST GENERATION HYBRIDS

Figure 19

On the left is the susceptible Turkish variety. On the right is the resistant Ambalema variety. In the center is the F_1 hybrid between the two varieties. The hybrid is as susceptible as the Turkish parent.

pothesis of duplicate factors, representing the 15:1 ratio was assumed in the analysis of the data. In the column Dev. ÷ P. E. in Table I, it is evident that all the progenies, except No. 3, gave results well within the limits of random sampling. On the basis of observations on the second generation, it can be concluded that the ratio of 15:1 holds in this case.

The backcross generation. Since susceptibility was shown to be dominant in the F_1, backcrosses were made to the resistant Ambalema. Both direct and reciprocal F_1 hybrids were backcrossed. If the hypothesis of 15:1 ratio for duplicate factors assumed from the evidence of the F_2 were true, then it would be expected that the backcross should give a ratio of 3 susceptible to one resistant plants.

That this was the case is shown by the results given in Table II. Of five backcross progenies, four showed clearly that the 3:1 relation holds. One progeny gave a deviation above the limit accounted to the error in sampling. Since there are four progenies in which the deviations are well inside the limits of random sampling, the deviation in that progeny may be attributed to differential mortality of the zygotes of the double recessive class or to the nonfunctioning of some of the gametes carrying the genes for resistance. In general it may be concluded that the backcross gives evidence in support of the 15:1 ratio.

The F_3 generation. The behavior of the third generation furnishes useful evidence in support or confirmation of the hypothesis developed on the basis of the second and backcross generations. Four selections were made in the F_2 from plants with only mild or no mosaic symptoms, and sixty from plants exhibiting the characteristic disease symptoms. The progenies from these were studied and the results are briefly summarized as follows:

SEGREGATION OF MOSAIC RESISTANCE IN THE SECOND GENERATION

Figure 20

Group of second generation (F_2) plants of cross between Turkish and Ambalema inoculated with mosaic virus. The large plant in the center is resistant to infection. All the other seedlings are susceptible. Experimental results show that resistance is conditioned by two independently inherited recessive factors, both of which must be present in duplicate (homozygous) for a plant to exhibit resistance.

The progenies from the four resistant plants were resistant. Thirteen progenies (190, 196, 200, 205, 207, 208, 211, 225, 230, 235, 236, 238 and 239) segregated on the basis of 15:1; susceptible to resistant. All these progenies showed deviations which can well be considered as due to random sampling. Of sixteen progenies for which a 3:1 ratio was assumed, thirteen (197, 203, 216, 223, 224, 227, 233, 240, 244, 255, 259, 260 and 262) exhibited low deviations while three (217, 241 and 249) showed odds higher than ordinarily admitted as due to random sampling.

Thirty-one progenies proved to be susceptible.*

The F_3 families were expected to behave, on the basis of the 15:1 ratio, as follows: 7 pure-breeding susceptible; 4 heterozygous, segregating on the basis of 15:1; 4 segregating on the basis of 3:1, and one pure-breeding resistant. That the observations conform to expectation is shown in Table III.

A simple examination of this table makes it clear that the probabilities are very high, that the deviations listed may be expected to occur by chance, i.e., due to error of sampling. The exact agreement in the case of the resistant families is due to the fact that their reaction was known at the time of selection.

It is concluded that the F_3 generation gives additional evidence supporting the theory that there is a 15:1 relationship of susceptibility to resistance in the cross *Ambalema* × *Turkish*.

Conclusions

The F_1 generation of *Ambalema* × *Turkish* and the reciprocal and other crosses, indicate that susceptibility to tobacco mosaic is dominant while resistance is recessive. The results of the F_2 generation, the backcrosses to both direct and reciprocal crosses, and the F_3 generation, indicate a relationship which leads to the conclusion that we are concerned here with a case of duplicate factors in which recessiveness of the two factors is represented by resistance, and susceptibility results when either one or the other, or both factors are in the dominant condition. If the resistance character were represented by $r_1r_1r_2r_2$ and susceptibility by $R_1R_1R_2R_2$, the first hybrid generation would be represented by $R_1r_1R_2r_2$. Resistance and susceptibility to mosaic may best be represented by adding *m* to the symbols, in order to distinguish this resistance or susceptibility from that to any other disease. Thus, the F_1 would be represented by $R_{m1}r_{m1}R_{m2}r_{m2}$ and the resistant parent by $r_{m1}r_{m1}r_{m2}r_{m2}$.

On the basis of the 15:1 ratio, the following genotypes and ratios are expected:

1	$R_{m1}R_{m1}R_{m2}R_{m2}$
2	$R_{m1}R_{m1}R_{m2}r_{m2}$
1	$R_{m1}R_{m1}r_{m2}r_{m2}$
2	$R_{m1}r_{m1}R_{m2}R_{m2}$
4	$R_{m1}r_{m1}R_{m2}r_{m2}$
2	$R_{m1}r_{m1}r_{m2}r_{m2}$
1	$r_{m1}r_{m1}R_{m2}R_{m2}$
2	$r_{m1}r_{m1}R_{m2}r_{m2}$
1	$r_{m1}r_{m1}r_{m2}r_{m2}$

Of the above, $R_{m1}r_{m1}R_{m2}r_{m2}$ are expected to segregate in the ratio of 15:1; $R_{m1}r_{m1}r_{m2}r_{m2}$ and $r_{m1}r_{m1}R_{m2}r_{m2}$ in the ratio of 3:1; while $r_{m1}r_{m1}r_{m2}r_{m2}$ is the double recessive, resistant; and all of the other genotypes are pure-breeding susceptible. The behavior of the F_3 families has given proof of duplicate factors. The expectations of seven pure-breeding susceptible; four segregating in the ratio of 15:1; four segregating in the ratio of 3:1; and one pure-breeding resistant was realized.

Practical Implications

The determination of the behavior of resistance or susceptibility to tobacco mosaic was regarded as a very important requirement in a program for improvement of tobacco by breeding for resistance to this disease. The fact that resistance proved to be recessive furnished an easy way of handling the segregates in the second and third and back-

* The tables on results of the F_3 generation are available to anyone desiring to examine them.

cross generations. Any resistant plants in these generations could be isolated as the basis of resistant lines. The recessiveness of resistance made it possible to eliminate all the susceptible plants in any of the segregating generations. Since only one out of every sixteen plants proved to be resistant, it was necessary to grow large progenies in order to increase the frequency with which resistant plants occurred. It was found that some F_3 families segregated in the proportion of three susceptible to one resistant; a relation similar to the backcross frequency. Therefore, these were further incorporated in the breeding program, because the frequency of resistant plants was increased four times over the corresponding frequency of the F_2 generation. In any breeding program in plant improvement it is well to handle large numbers in order that the desired qualities may be combined in one or a few lines. In tobacco, where we have to deal with 24 pairs of chromosomes one must certainly cope with a not very simple situation and one in which the solution of economic problems will not be easy.*

Summary

1. In crosses between mosaic-susceptible and mosaic-resistant varieties of tobacco, the F_1 generation is susceptible, indicating recessiveness of the resistant character.

2. On the basis of evidence from the F_2, F_3 and backcross progenies of crosses between resistant and susceptible varieties, it is concluded that duplicate factors are responsible for the mechanism of inheritance of susceptibility and resistance to mosaic.

3. Resistance results only when the two factors are in the recessive condition.

4. The duplicate factors are designated by the formula $R_{m1}r_{m1}R_{m2}r_{m2}$.

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Table I. Behavior of the F_2 Generation of Crosses upon Infection with Mosaic

Progeny	n	Mosaic Reaction	Frequencies Observed	Calculated n	Calculated Ratio	Dev.	P.E.	Dev./P.E.
Am X T	2145	S	2010	2022.94	15:1	0.94	±7.56	0.12
		R	135	134.06				
T x Am	911	S	855	856.06	15:1	0.94	±4.93	0.19
		R	56	56.94				
685	624	S	600	585.00	15:1	15.00	±4.08	3.68
		R	24	39.00				
690	2456	S	2296	2302.50	15:1	4.50	±6.09	0.56
		R	158	153.50				
715	482	S	456	451.88	15:1	4.12	±3.88	1.15
		R	26	30.12				
716	563	S	527	527.81	15:1	0.81	±3.63	0.22
		R	36	35.19				

Table II. Behavior of Backcross Progenies of the F_1 Generation of Direct and Reciprocal Crosses.

Progeny	n	Mosaic Reaction	Observed	Calculated n	Calculated Ratio	Dev.	P.E.	Dev./P.E.
(Am x T) x Am	878	S	671	658.38	3:1	14.50	±6.65	1.66
		R	205	219.50				
(T x Am) x Am	1351	S	1051	1013.25	3:1	37.75	±10.75	3.52
		R	300	337.75				
685 x Am	372	S	263	279.00	3:1	16.00	±6.63	2.84
		R	109	93.00				
715 x Am	379	S	280	284.25	3:1	10.75	±5.69	2.77
		R	79	94.75				
716 x Am	338	S	248	249.00	3:1	1.00	±5.32	0.19
		R	84	83.00				

Table III. Distribution of F_3 Families on the Basis of their reaction to Mosaic and with respect to Segregation of Susceptibility and Resistance in the Ratio of 15:1

Class	Observed Frequencies	Theoretical Ratio	Observed Ratio	P.E.	Dev./P.E.	Probability in 100
Susceptible	51	7	7.75	±0.6340	1.18	41.97
15:1	13	4	3.25	± .8841	1.89	38.81
3:1	16	4	4.00	± .8841	0	
Resistant	4	1	1.00	± .4842	0	
Total	64	16	16.00			

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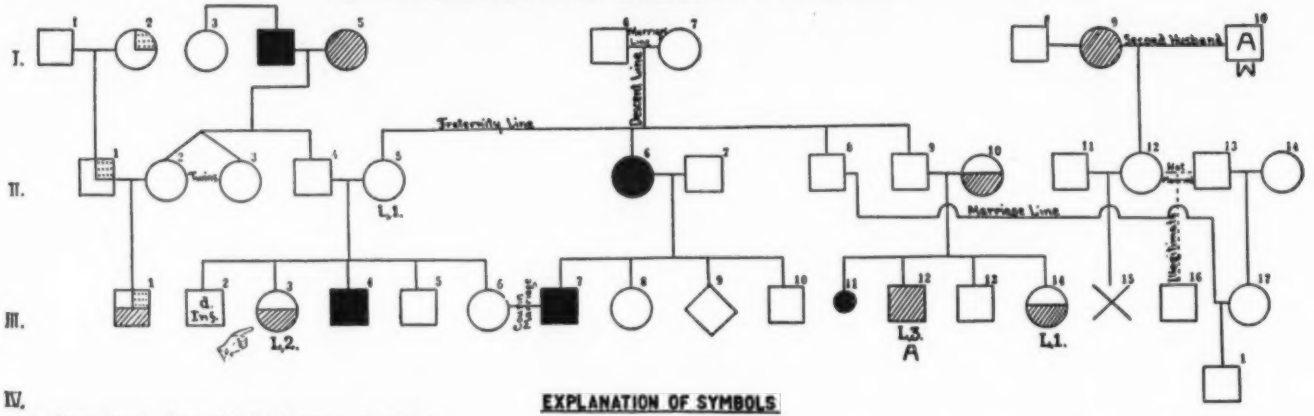
SAMPLE PEDIGREE CHART SHOWING THE MANNER OF CONSTRUCTION, AND THE USE OF STANDARD AND SPECIAL SYMBOLS.



EXPLANATION OF SYMBOLS

(a) Standard for all Pedigree Charts:

□=Male; ○=Female; ◇=Sex unknown; ●=Still-birth or Miscarriage; X=Children — number and sex unknown; ○○=Twins; d. Inf.=Died in Infancy; Points to the Propositus or central figure in the pedigree.

□○=Parents.

□○□○○=Children.

Roman figures to the left indicate generations; Arabic figures locate individuals, (thus III. 7 is the young man in the third generation who married his cousin).

The following letters, placed in or around the individual's pedigree symbol, are standard for certain traits: A, alcoholic; B, blind; D, deaf; E, epileptic, F, feebleminded, I, insane, M, migraineous; N, normal in reference to traits under consideration; Ne, neurotic; P, paralytic; Sx, sexually immoral; S, syphilelic; T, tuberculous; W, wanderer.

(b) Especially devised or selected for this particular pedigree-chart:

■ ● = Successful leaders in politics. ◱ ◷ = Extra thumb on right hand. L.1.=Highly successful author. L.3.=Little or no ability in literary efforts. ▨ ◍ = Superior in vocal music. ▨ ◍ = Medium attainment in vocal music.

To fit the particular family and traits (whether physical, mental or temperamental; good or bad) under consideration, invent special symbols, or select special letters (in addition to those standardized under (a) above) to be placed within or near the particular individual's pedigree symbol, to indicate particular traits and their degree of development.

Prepared by the International Commission of Eugenics. See *Journal of Heredity* for August 1926. Additional copies may be obtained from A.G.A.

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